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THE UNIVERSITY OF ALBERTA

Systematics of the genus group taxa of the Siphonini (Diptera: Tachinidae)

by

©

James E. O'Hara

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Doctor of Philosophy

Department of Entomology

EDMONTON, ALBERTA

Spring 1987

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Systematics of the genus group taxa of the Siphonini (Diptera: Tachinidae) submitted by James E. O'Hara in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

The Siphonini are a monophyletic tribe of about 300 described species. The genera and subgenera of the tribe are revised for the world fauna, based on study of adults of most described and more than 100 undescribed species, and first instars of about 70 species. Seven genera are recognized, each presumed to be monophyletic: *Goniocera* Brauer and Bergenstamm, *Proceromyia* Mesnil (elevated from subgeneric status within *Ceromya* and including *Nipponoceromyia* Mesnil and Shima, n. syn.), *Entomophaga* Lioy, *Ceromya* Robineau-Desvoidy (including new synonym *Actinactia* Townsend), *Actia* Robineau-Desvoidy, *Peribaea* Robineau-Desvoidy and *Siphona* Meigen. *Ceromya* is informally divided into *Ceromya s.s.* and the *Ceromya silacea* species group. *Siphona* Meigen is reclassified into nine subgenera: *Actinocrocuta* Townsend (new status), *Aphantorhapha* Townsend (new status), *Aphantorhaphopsis* Townsend (new status; an unresolved and possibly polyphyletic group of Old World species, including *Asiphona* Mesnil, n. syn.), *Baeomyia* O'Hara (new status), *Ceranthia* Robineau-Desvoidy (new status), *Pseudosiphona* Townsend (new status), *Siphona* Meigen, *Siphonopsis* Townsend (new status) and *Uruactia* Townsend (new status). Two New World species, *Actia panamensis* Curran and *Aphantorhapha pulla* Reinhard are left unplaced in *Siphona s.l.* Three species groups, and a group of unrelated and unplaced species, of undescribed New World *Siphona s.l.* species are reviewed but not formally named or described. *Actia heterochaeta* Bezzi is left unplaced within the Siphonini. Removed from the Siphonini is *Actia aberrans* Malloch. Four species names are reduced to synonyms, three are elevated from subspecific to specific status, and lectotypes are designated for *Ceromya cibdela* (Villeneuve) and *S. (Pseudosiphona) brevirostris* Coquillett.

A chapter about structural features of the Siphonini is followed by a key to genera and subgenera of the world and diagnoses of genera and subgenera. A list of siphonine hosts details known host preferences within the Siphonini.

A cladistic analysis based on ingroup (Siphonini) and outgroup (Tachinidae) comparisons is used to partially reconstruct the phylogenetic history of the major siphonine lineages.

Geographic distribution of siphonine genera and subgenera is discussed in relation to historical events during earth history and the presumed phylogenetic history of the Siphonini.

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Table of Contents

Chapter Page

1. INTRODUCTION 1

2. MATERIALS AND METHODS 3

2.1 Materials 3

2.2 Methods 8

2.2.1 Ranking of taxa 8

2.2.2 Treatment of undescribed species 10

2.2.3 Terms 11

2.2.4 Examination and illustration of specimens 12

2.2.5 Genitalic dissections 12

2.2.6 Preparation of first instars 13

3. STRUCTURAL FEATURES 15

3.1 Historical review 15

3.2 Structural features of the Siphonini 16

4. CLASSIFICATION OF THE SIPHONINI 43

4.1 List of major references to the Siphonini 43

4.2 Diagnosis of Siphonini Rondani 43

4.3 Review of major keys to genera and subgenera of the Siphonini 45

4.4 Key to adults of the supraspecific taxa and selected species of world Siphonini ... 47

4.5 Notes about classification chapter 53

4.5.1 Notes about lists of included species 53

4.5.2 Summary of taxonomic changes 54

4.5.3 Type designations of Coquillett and Townsend 55

4.6 Goniocera Brauer and Bergenstamm 56

4.7 Proceromyia Mesnil 62

4.8 Entomophaga Lioy 66

4.9 Ceromya Robineau-Desvoidy sensu lato 72

4.10 *Ceromya* Robineau-Desvoidy *sensu stricto* 74

4.11 *Ceromya silacea* (Meigen) species group 89

4.12 *Actia* Robineau-Desvoidy 94

4.13 *Peribaea* Robineau-Desvoidy 110

4.14 *Siphona* Meigen 120

4.15 *Siphona* (*Actinocrocuta* Townsend) 121

4.16 *Siphona* (*Aphantorhapha* Townsend) 125

4.17 *Siphona* (*Aphantorhaphopsis* Townsend) 129

4.18 *Siphona* (*Baeomyia* O'Hara) 137

4.19 *Siphona* (*Ceranthia* Robineau-Desvoidy) 141

4.20 *Siphona* (*Pseudosiphona* Townsend) 147

4.21 *Siphona* (*Siphona* Meigen) 155

4.22 *Siphona* (*Siphonopsis* Townse[illegible]) 171

4.23 *Siphona* (*Uruactia* Townsend) 177

4.24 New and described New World species unplaced to subgenus in *Siphona* *s.l.* 179

- 4.24.1 New World *Siphona* species group 1 179
- 4.24.2 New World *Siphona* species group 2 181
- 4.24.3 New World *Siphona* species group 3 182
- 4.24.4 Unplaced New World species of *Siphona* 184

4.25 *Actia heterochaeta* Bezzi, unplaced species of Siphonini 187

5. HOSTS 264

5.1 Hosts 264

- 5.1.1 Explanation of parasite-host list 264

6. EVOLUTION OF THE SIPHONINI 276

6.1 Introduction 276

6.2 Monophyly of the Siphonini 279

6.3 Monophyly of genera and subgenera 280

6.4 Monophyly of the Proceromyia Mesnil and Entomophaga Lioy lineage 289

6.5 Monophyly of the Peribaea R.-D. and Siphona Meigen lineage 289

6.6 Phylogenetics of non-Siphona s.l. siphonine lineages 290

6.7 Phylogenetics of Siphona subgenera 293

6.8 Evolutionary trends 306

6.9 Historical zoogeography 310

7. CONCLUDING REMARKS 326

8. LITERATURE CITED 327

List of Tables

Table Page

1. Distribution of character states in the Siphonini.........37
2. Parasite-host list for world Siphonini.........266
3. Tachinid species examined for outgroup comparison with the Siphonini.........278

List of Figures

Figure Page

1. Head profile of male *Goniocera io* 189
2. Head profile of male *Proceromyia macronychia* 189
3. Head profile of male *Proceromyia pubioculata*. 189
4. Head profile of male *Entomophaga exoleta*. 189
5. Head profile of male *Entomophaga nigrohalterata* 191
6. Head profile of male *Ceromya flaviceps*. 191
7. Head profile of male *Ceromya* New Guinea sp. 15 191
8. Head profile of male *Actia lamia*. 191
9. Head profile of male *Actia* Nepal sp. 1. 193
10. Head profile of male *Actia parviseta* 193
11. Head profile of male *Peribaea cervina* 193
12. Head profile of male *Peribaea tibialis*. 193
13. Head profile of male *Siphona (Actinocrocuta) singularis* complex. 195
14. Head profile of male *Siphona (Aphantorhapha) arizonica*. 195
15. Head profile of male *Siphona (Baeomyia) xanthogaster*. 195
16. Head profile of male *Siphona (Ceranthia) flavipes*. 195
17. Head profile of male *Siphona (Pseudosiphona) brevirostris* 197
18. Head profile of male *Siphona (Siphonopsis) plusiae*. 197
19. Head profile of male *Siphona s.l.*, sp. grp. 2, sp. 1. 197
20. Head profile of male *Siphona s.l.*, unplaced sp. 23. 197
21. Wing of *Actia interrupta*, with wing veins labelled 199
22. Wing of *Siphona (Baeomyia) xanthogaster*. 199
23. Proboscis of *Actia diffidens* 201
24. Proboscis of *Siphona (Siphonopsis) plusiae*. 201
25. Proboscis of *Siphona (Siphona) maculata* 201

26. Proboscis of *Siphona (Siphona) pisinnia*. 201

27. *Peribaea* sp., illustrating two strong and opposed proepimeral setae. 201

28. *Siphona (Siphona) maculata*, illustrating single strong proepimeral seta. 201

29. Labella of *Actia diffidens*, illustrating padlike condition and numerous pseudotracheae. 201

30. Labella of *Siphona (Siphonopsis) plusiae*, illustrating elongate condition and relatively few pseudotracheae. 201

31. *Actia diffidens*, illustrating short lower katepisternal seta and two anepisternal setulae. 203

32. *Siphona (Siphona) maculata*, illustrating long lower katepisternal seta and single anepisternal setula. 203

33. *Actia diffidens*, illustrating row of hairs on katepisternum anterior to mid coxa. 203

34. *Siphona (Siphona) maculata*, illustrating presence of several hairs on katepisternum restricted to midline region. 203

35. *Ceromya varichaeta*, illustrating patch of tiny hairs on anterior surface of mid femur. 203

36. *Siphona (Siphona) maculata*, illustrating typical condition of anterior surface of mid femur. 203

37. *Ceromya varichaeta*, illustrating presence of strong anterodorsal seta on mid tibia. 203

38. *Siphona (Baeomyia) xanthogaster*, illustrating absence of anterodorsal seta on mid tibia. 203

39. Lateral view of pregonite of *Ceromya americana* complex. 205

40. Ventrolateral view of pregonite of *Ceromya americana* complex. 205

41. Lateral view of pregonite of *Actia diffidens*. 205

42. Ventral view of pregonite of *Actia diffidens*. 205

43. Ventral view of female genitalia of *Siphona (Siphona) maculata*. 205

44. Ventral view of female genitalia of *Siphona (Ceranthia) flavipes*. 205

45. Lateral view of female genitalia of *Siphona (Siphona) maculata*. 205

46. Lateral view of female genitalia of *Siphona (Ceranthia) flavipes*................... 205

47. Male sternum 5 of *Goniocera schistacea*. 207

48. Male sternum 5 of *Proceromyia macronychia*.. 207

49. Male sternum 5 of *Proceromyia pubioculata*. 207

50. Male sternum 5 of *Entomophaga exoleta*. 207

51. Male sternum 5 of *Entomophaga nigrohalterata*.................................... 207

52. Male sternum 5 of *Ceromya silacea*.. 207

53. Male sternum 5 of *Ceromya flaviceps*. 207

54. Male sternum 5 of *Ceromya* New Guinea sp. 18.................................... 207

55. Male sternum 5 of *Ceromya americana* complex. 207

56. Male sternum 5 of *Ceromya amblycera*. 207

57. Male sternum 5 of *Ceromya lutea*. 207

58. Male sternum 5 of *Actia lamia*.. 207

59. Male sternum 5 of *Actia autumnalis*. 209

60. Male sternum 5 of *Peribaea apicalis*.. 209

61. Male sternum 5 of *Peribaea* Australia sp. 1.. 209

62. Male sternum 5 of *Siphona (Actinocrocuta) singularis* complex.................... 209

63. Male sternum 5 of *Siphona (Aphantorhapha) arizonica*. 209

64. Male sternum 5 of *Siphona (Aphantorhaphopsis)* Nepal sp. 1. 209

65. Male sternum 5 of *Siphona (Ceranthia) flavipes*. 209

66. Male sternum 5 of *Siphona (Pseudosiphona)* sp. 4. 209

67. Male sternum 5 of *Siphona (Siphona) geniculata*. 209

68. Male sternum 5 of *Siphona (Uruactia)* sp. 31.. 209

69. Male sternum 5 of *Siphona s.l.*, sp. grp. 1, sp. 28.................................. 209

70. Male sternum 5 of *Siphona s.l.*, sp. grp. 2, sp. 9. 209

71. Male pregonite of *Goniocera io*. 211

72. Male pregonite of *Goniocera versicolor*. 211

73. Male pregonite of *Proceromyia macronychia*. 211

74. Male pregonite of *Proceromyia pubioculata*. 211

75. Male pregonite of *Entomophaga exoleta*. 211

76. Male pregonite of *Entomophaga nigrohalterata*. 211

77. Male pregonite of *Ceromya flaviceps*. 211

78. Male pregonite of *Ceromya* New Guinea sp. 6. 211

79. Male pregonite of *Ceromya americana* complex. 211

80. Male pregonite of *Ceromya cornuta*. 213

81. Male pregonite of *Ceromya* Mexico sp. 5. 213

82. Male pregonite of *Ceromya* Brazil sp. 3. 213

83. Male pregonite of *Ceromya lutea*. 213

84. Male pregonite of *Ceromya silacea*. 213

85. Male pregonite of *Actia lamia*. 213

86. Male pregonite of *Actia diffidens*. 213

87. Male pregonite of *Peribaea tibialis*. 213

88. Male pregonite of *Peribaea* Australia sp. 3. 213

89. Male pregonite of *Siphona (Actinocrocuta) singularis* complex. 215

90. Male pregonite of *Siphona (Aphantorhapha) arizonica*. 215

91. Male pregonite of *Siphona (Aphantorhaphopsis) crassulata*. 215

92. Male pregonite of *Siphona (Aphantorhaphopsis) starkei*. 215

93. Male pregonite of *Siphona (Baeomyia) xanthogaster*. 215

94. Male pregonite of *Siphona (Ceranthia) flavipes*. 215

95. Male pregonite of *Siphona (Pseudosiphona) brevirostris*. 215

96. Male pregonite of *Siphona (Siphona) geniculata*. 215

97. Male pregonite of *Siphona (Siphonopsis) plusiae*. 215

98. Male pregonite of *Siphona (Siphonopsis)* sp. N. 217

99. Male pregonite of *Siphona (Uruactia)* sp. 31. 217

100. Male pregonite of *Siphona s.l.*, sp. grp. 1, sp. 27 217
101. Male pregonite of *Siphona s.l.*, sp. grp. 1, sp. 28 217
102. Male pregonite of *Siphona s.l.*, sp. grp. 2, sp. 1 217
103. Male pregonite of *Siphona s.l.*, sp. grp. 2, sp. 2 217
104. Male pregonite of *Siphona s.l.*, sp. grp. 3, sp. 3 217
105. Male pregonite of *Siphona s.l.*, sp. grp. 3, sp. 22 217
106. Male pregonite of *Siphona s.l.*, unplaced sp. 1 217
107. Male distiphallus of *Goniocera io* 219
108. Male distiphallus of *Proceromyia macronychia* 219
109. Male distiphallus of *Proceromyia pubioculata* 219
110. Male distiphallus of *Entomophaga exoleta* 219
111. Male distiphallus of *Entomophaga nigrohalterata* 219
112. Male distiphallus of *Ceromya silacea* 219
113. Male distiphallus of *Ceromya flaviceps* 221
114. Male distiphallus of *Ceromya americana* complex 221
115. Male distiphallus of *Ceromya cornuta* 221
116. Male distiphallus of *Ceromya lutea* 221
117. Male distiphallus of *Actia lamia* 221
118. Male distiphallus of *Actia autumnalis* 221
119. Male distiphallus of *Actia* New World sp. 4 223
120. Male distiphallus of *Peribaea apicalis* 223
121. Male distiphallus of *Peribaea fissicornis* 223
122. Male distiphallus of *Siphona (Actinocrocuta) singularis* complex 223
123. Male distiphallus of *Siphona (Actinocrocuta)* sp. 1 223
124. Male distiphallus of *Siphona (Aphantorhapha) arizonica* 223
125. Male distiphallus of *Siphona (Aphantorhaphopsis) nigronitens* 225
126. Male distiphallus of *Siphona (Baeomyia) hurdi* 225
127. Male distiphallus of *Siphona (Ceranthia) flavipes* 225

128. Male distiphallus of *Siphona (Pseudosiphona)* sp. 1 225

129. Male distiphallus of *Siphona (Siphona) geniculata* 225

130. Male distiphallus of *Siphona (Siphonopsis) plusiae* 225

131. Male distiphallus of *Siphona (Uruactia)* sp. 31. 227

132. Male distiphallus of *Siphona s.l.*, sp. grp. 1, sp. 25. 227

133. Male distiphallus of *Siphona s.l.*, sp. grp. 2, sp. 1. 227

134. Male distiphallus of *Siphona s.l.*, sp. grp. 2, sp. 3. 227

135. Male distiphallus of *Siphona s.l.*, sp. grp. 3, sp. 3. 227

136. Male distiphallus of *Siphona s.l.*, unplaced sp. 1 227

137. Male surstylus and cerci of *Goniocera io*. 229

138. Male surstylus and cerci of *Ceromya americana* complex. 229

139. Male surstylus and cerci of *Peribaea apicalis*. 229

140. Male surstylus and cerci of *Siphona (Pseudosiphona)* sp. 1 229

141. Male surstylus and cerci of *Siphona (Siphona) geniculata* 229

142. Posterior view of male genitalia of *Siphona (Actinocrocuta) singularis* complex 229

143. Posterior view of male genitalia of *Siphona (Aphantorhapha)* sp. 1. 229

144. Posterior view of male genitalia of *Siphona (Siphona) kairiensis* 229

145. Female genitalia of *Goniocera io* 231

146. Female genitalia of *Proceromyia macronychia*. 231

147. Female genitalia of *Entomophaga nigrohalterata* 231

148. Female genitalia of *Ceromya silacea*. 231

149. Female genitalia of *Ceromya flaviceps*. 233

150. Female genitalia of *Ceromya ontario* 233

151. Female genitalia of *Actia interrupta* 233

152. Female genitalia of *Actia* Zaire sp. 1. 233

153. Female genitalia of *Peribaea fissicornis*. 235

154. Female genitalia of *Peribaea* Africa sp. 5. 235

155. Female genitalia of *Peribaea ugandana*. 235
156. Female genitalia of *Peribaea* Australia sp. 1. 235
157. Lateral view of first instar of *Ceromya americana* complex, with ventral view of abdominal segments 7 to 9. 237
158. First instar of *Goniocera io*. 237
159. First instar of *Entomophaga nigrohalterata*. 237
160. First instar of *Ceromya silacea*. 239
161. First instar of *Ceromya palloris*. 239
162. First instar of *Ceromya americana* complex. 239
163. First instar of *Ceromya americana* complex. 239
164. First instar of *Ceromya* Australia sp. 3. 241
165. First instar of *Ceromya* Nepal sp. 4. 241
166. First instar of *Ceromya* Chile sp. 1. 241
167. First instar of *Ceromya* Brazil sp. 5. 241
168. First instar of *Actia diffidens*. 243
169. First instar of *Actia lamia*. 243
170. First instar of *Actia malaisei*. 243
171. First instar of *Actia* nr. *parviseta*. 243
172. First instar of *Peribaea ugandana*. 245
173. First instar of *Peribaea* Africa sp. 3. 245
174. First instar of *Peribaea* Africa sp. 4. 245
175. First instar of *Peribaea* Africa sp. 5. 245
176. First instar of *Siphona (Aphantorhaphopsis)* Australia sp. 1. 247
177. First instar of *Siphona (Aphantorhaphopsis)* Kenya sp. 1 247
178. First instar of *Siphona (Aphantorhaphopsis)* Nepal sp. 1. 247
179. First instar of *Siphona (Aphantorhaphopsis)* Nepal sp. 4. 247
180. First instar of *Siphona (Aphantorhaphopsis)* Uganda sp. 1. 249
181. First instar of *Siphona (Aphantorhaphopsis)* South Africa sp. 1. 249

182. First instar of *Siphona (Actinocrocuta) singularis* complex.......................... 249
183. First instar of *Siphona (Aphantorhapha) arizonica*.......................... 249
184. First instar of *Siphona (Baeomyia) sonorensis*.......................... 251
185. First instar of *Siphona (Ceranthia) flavipes*.......................... 251
186. First instar of *Siphona (Ceranthia)* U.S. sp. 1.......................... 251
187. First instar of *Siphona (Ceranthia)* U.S. sp. 7.......................... 251
188. First instar of *Siphona (Pseudosiphona)* sp. 1.......................... 253
189. First instar of *Siphona (Pseudosiphona)* sp. 2.......................... 253
190. First instar of *Siphona (Pseudosiphona)* sp. 14.......................... 253
191. First instar of *Siphona (Pseudosiphona)* sp. 15.......................... 253
192. First instar of *Siphona (Pseudosiphona)* sp. 16.......................... 255
193. First instar of *Siphona (Pseudosiphona)* sp. 17.......................... 255
194. First instar of *Siphona (Siphonopsis) plusiae*.......................... 255
195. First instar of *Siphona (Siphonopsis) conata*.......................... 255
196. First instar of *Siphona (Siphona) lutea*.......................... 257
197. First instar of *Siphona (Siphona) nigricans*.......................... 257
198. First instar of *Siphona (Siphona)* sp. 1.......................... 257
199. First instar of *Siphona s.l.*, sp. grp. 1, sp. 24.......................... 257
200. First instar of *Siphona s.l.*, sp. grp. 1, sp. 27.......................... 259
201. First instar of *Siphona s.l.*, sp. grp. 1, sp. 30.......................... 259
202. First instar of *Siphona s.l.*, sp. grp. 2, sp. 3.......................... 259
203. First instar of *Siphona s.l.*, sp. grp. 3, sp. 3.......................... 259
204. First instar of *Siphona s.l.*, unplaced, sp. 1.......................... 261
205. First instar of *Siphona s.l.*, unplaced, sp. 2.......................... 261
206. First instar of *Siphona s.l.*, unplaced, sp. 10.......................... 261
207. First instar of *Siphona s.l.*, unplaced, sp. 14.......................... 261
208. First instar of *Siphona s.l.*, unplaced, sp. 20.......................... 263
209. First instar of *Siphona s.l.*, unplaced, sp. 23.......................... 263

210. Cladistic relationships and geographic distribution of the genera and subgenera of the Siphonini. 299

211. Distribution of states for five characters relevant to the interpretation of the cladistic relationships of *Goniocera* B. & B. 301

212. Cladistic relationship of *Goniocera* based on long preapical *ad* on fore tibia as an apotypic state 303

213. Cladistic relationship of *Goniocera* based on independent evolution of spinules on the male pregonite of *Goniocera io* and *Ceromya s.s.* species 303

214. *Goniocera* and *Ceromya s.s.* as sister groups based on spinules on male pregonite as synapotypy. 303

215. *Goniocera* as derived subgroup of *Ceromya s.s.*, based on one interpretation of spinules on male pregonite as synapotypy. 303

216. One interpretation of the cladistic relationships within *Siphona s.l.*, based on presence of a seta posteriorly on male pregonite as synapotypy. 305

217. One interpretation of the cladistic relationships within *Siphona s.l.*, based on presence of spinules on the sclerotized portion of male pregonite as synapotypy 305

218. Correlation between position of wing crossvein *dm-cu* and length of wing vein CuA_1. 309

219. General zoogeographic history of Nearctic elements of the Siphonini. 323

220. Pre-Pliocene zoogeographic history of Neotropical Siphonini. 325

1. INTRODUCTION

The tribe Siphonini is a monophyletic taxon of about 300 described species of uncertain phylogenetic position within the Tachinidae (some authors favoring its placement in the Goniinae, others the Tachininae). Adults are smaller than most tachinid flies, generally 3-5mm in length, and as larvae are almost exclusively parasitoids of larval Lepidoptera. Siphonines are widely distributed throughout the world, with greatest diversity in the non-humid tropics.

Mesnil established the modern concept of the Siphonini (as Siphonina) in his illustrious tachinid contribution to "Die Fliegen der palaearktischen Region" (1962-5). Prior to that time, several genera now relegated to the Neaerini were included because of their external similarity to members of the Siphonini (*e.g.* Mesnil 1939, 1954; van Emden, 1954). Herting, in his interpretive survey of female genitalia in the Calyptratae (1957), was first to recognize the error in this classification and his findings were subsequently incorporated into Mesnil's (1962-5) revision of the Palearctic Siphonini. Crosskey maintained Mesnil's concept of the tribe in his treatments of the tachinid faunas of the Australian (1973), Oriental (1976a) and Afrotropical (1980) regions, as did Andersen (1983) in his recent revision of the Old World Siphonini and Herting (1984) in his catalogue of Palearctic Tachinidae.

In marked contrast to the recent attention conferred upon Old World siphonines, the New World fauna is without a modern treatment at any level. Townsend's revision of the "Siphonini" and "Actiini" in his "Manual of Myiology" (1940) is an untenable classification comprising a heterogeneous and polyphyletic assemblage of genera. A valuable step toward a modern classification of North American Siphonini was achieved by Sabrosky and Arnaud (1965). These authors brought together almost all of the siphonine taxa of America north of Mexico within their subtribe of the Siphonini, the Siphonina, but included as well a number of unrelated genera. Guimarães (1971) catalogued the tachinids of America south of the United States, and though following the broad concept of the Siphonini advanced by Sabrosky and Arnaud, he did not similarly recognize subtribes. Consequently his genera of the Siphonini *sensu* Mesnil are interspersed with a variety of unrelated taxa.

This study was undertaken with the aim of revising the supraspecific taxa of the Siphonini, in particular reclassifying the New World siphonines in light of recent advances concerning the Old World fauna. This aim has been tempered somewhat by the diverse and largely undescribed fauna of the Neotropics, which requires detailed study and description of species before a satisfactory supraspecific classification can be established. The results of a preliminary study of many undescribed Neotropical species is included here as an aid to future systematic research on the Neotropical Siphonini.

In addition to revising the Siphonini and providing a framework about which future revisions of genera can proceed, this work is also an exploration into the evolutionary history of the tribe in terms of phylogenetic relationships among the supraspecific taxa and character state diversity among species. To attain this goal, most available types and specimens of many undescribed species were examined. Based as it is upon patterns of character state distribution, this work is as much a study of evolutionary patterns in the Siphonini and their explanation as it is a taxonomic revision.

Included in this paper are lists of species names of the Siphonini, arranged according to a revised classification of the tribe. A key to, and descriptions of, the supraspecific taxa are provided. Known hosts of the Siphonini are listed. Character state diversity is tabulated and discussed, and the evolutionary history of the supraspecific taxa analyzed.

2. MATERIALS AND METHODS

2.1 Materials

This paper is based on the morphological study of adult specimens of about 270 described species (about 90% of the described world fauna) and more than 100 undescribed species, including study of male genitalia of more than 250 species and female genitalia of about 90 species. First instars of about 70 species were also examined.

Codes used in the text for designating institutions and private collections appear below with the names of their respective curators.

AMNH	Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024; the late P. Wygodzinsky and K.A. Schmidt.
BLKU	Biological Laboratory, College of General Education, Kyushu University, Ropponmatsu, Fukuoka 810, Japan; H. Shima.
BMNH	Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD; R.W. Crosskey and A.C. Pont.
BPBM	Department of Entomology, Bernice P. Bishop Museum, P.O. Box 6037, Honolulu, HI 96818; N.L. Evenhuis.
CAS	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118; P.H. Arnaud, Jr.
CEA	Colección de la Estación Experimental Agronómica, Universidad de Chile, Maipú, Chile.
CIE	Colección del Centro de Investigacions Entomológicas, Universidad de Chile, Santiago, Chile; J. Herrera.

CNC	Biosystematics Research Centre [formerly Institute], Central Experimental Farm, K.W. Neatby Building, Ottawa, Ontario K1A 0C6; D.M. Wood.
DEI	Institut für Pflanzenschutzforschung Kleinmachnow, [formerly the Deutsches Entomologisches Institut], Akademie der Landwirtschaftswissenschaften, Bereich Eberswalde, 13 Eberswalde-Finow 1, Schicklerstrasse 5, German Democratic Republic; H.J. Müller and R. Gaedike.
DPI	Entomology Branch, Department of Primary Industries, Meiers Road, Indooroopilly, 4068, Queensland, Australia; B. Cantrell.
ETH	Entomologisches Institut, Eidgenössische Technische Hochschule, Zentrum, CH-8092 Zurich, Switzerland; W. Sauter.
FRI	Forest Research Institute, Dehra Dun, Uttar Pradesh, India. (I was unable to establish contact with this institution.)
FSF	Forschungsinstitut Senckenberg, Senckenberganlage 25, D-6000 Frankfurt 1, Federal Republic of Germany; J. Rademacher.
HDE	Hope Department of Entomology, University Museum, Oxford, OX1 3PW, England; M.J. Scoble.
HNHM	Zoological Department, Hungarian Natural History Museum, H-1088 Budapest, Baross u. 13, Hungary; F. Mihályi.
INPA	Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, 69.000 Manaus, Amazonas, Brazil; J.A. Rafael.
IRSN	Institut Royal des Sciences Naturelles de Belgique, Rue Vautier 31, B-1040 Bruxelles, Belgium.
JEOH	Private collection of the author.

MBR	División Entomología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Avenida Angel Gallardo 470, Buenos Aires, Argentina; A.O. Bachmann.
MCSN	Museo Civico di Storia Naturale, 20121 Milano, Corso Venezia 55, Italy; C. Leonardi.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138; M.K. Thayer.
MNHN	Entomologie, Muséum National d'Historie Naturelle, 45 bis Rue Buffon, Paris Ve, France; L. Matile.
MRAC	Entomology Section, Musée Royal de l'Afrique Centrale, B-1980, Tervuren, Belgium; E. De Coninck.
MSU	Department of Entomology, Michigan State University, East Lansing, MI 48824; R.L. Fischer.
MZF	Museo Zoologico de "La Specola", Università Degli Studi, Via Romana, 17-50125 Firenze, Italy; S. Mascherini.
NMBA	Naturhistorisches Museum der Benediktiner-Abtei Admont, A-8911 Admont, Austria; B. Hubl.
NMV	Entomology Department, Naturhistorisches Museum, Zoologische Abteilung, A-1014 Vienna, Burgring 7, Austria; R. Contreras-Lichtenberg.
NRS	Entomology Section, Swedish Museum of Natural History, S-10405 Stockholm, Sweden; P.I. Persson.
OSU	Department of Entomology, Oregon State University, Corvallis, OR 97331; M.D. Schwartz.

PHA	Private collection of P.H. Arnaud, Jr., c/o CAS.
PPRI	Department of Agriculture, Plant Protection Research Institute, National Collection of Insects, Private Bag X134, Pretoria 0001, Republic of South Africa; M.W. Mansell.
SMNS	Staatl. Museum für Naturkunde, Rosenstein 1, D-7000 Stuttgart 1, Federal Republic of Germany; B. Herting.
SPHTM	Entomology Section, School of Public Health and Tropical Medicine, Sydney University 2006, Sydney, New South Wales, Australia; M.L. Debenham.
UASM	Department of Entomology, Strickland Museum, University of Alberta, Edmonton, Alberta T6G 2E3; G.E. Ball.
UAT	Department of Entomology, University of Arizona, Tucson, AZ 85721; F.G. Werner.
UCB	Division of Entomology and Parasitology, University of California, Berkeley 4, CA 94720; J.A. Chemsak.
UCD	Department of Entomology, University of California, Davis, CA 95616; R.O. Schuster.
UCR	Department of Entomology, University of California, Riverside, CA 92521; S.I. Frommer.
UCS	Facultad de Agronomía, Universidad de Chile, Casilla 1004, Santiago, Chile; R. Cortés.
UKL	Department of Entomology, Snow Entomology Museum, University of Kansas, Lawrence, KS 66045; C.D. Michener and G.W. Byers.

UNH	Department of Entomology, University of New Hampshire, Durham, NH 03824; J.F. Burger.
UNLP	Division de Entomologia, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque, 1900 La Plata, Argentina; L. de Santis.
USNM	Systematic Entomology Laboratory, SEA, U.S. Department of Agriculture, United States National Museum, Washington, DC 20560; C.W. Sabrosky (retired) and N.E. Woodley.
USP	Museu de Zoologia, Universidad de São Paulo, Avenida Nazare, 481, Caixa Postal 7172, 04263, São Paulo, sp, Brazil; J.H. Guimarães.
UZI	Department of Zoology, Zoological Museum, Helgonavägen 3, S-223 62, Lund, Sweden; R. Danielsson.
WLD	Private collection of W.L. Downes, c/o MSU.
WSUP	Department of Entomology, James Entomological Collection, Washington State University, Pullman, WA 99164; W.J. Turner.
ZIL	Zoological Institute, USSR Academy of Sciences, Leningrad 199164, USSR; V.A. Richter.
ZMA	Instituut voor Taxonomische Zoölogie, Zoölogisch Museum, Universiteit van Amsterdam, Afdeling Entomologie, Plantage Middenlaan 64, 1018 DH Amsterdam, Netherlands; T. van Leeuwen.
ZMHU	Museum für Naturkunde an der Humboldt-Universität zu Berlin, Bereich Zoologisches Museum, DDR 104 Berlin, Invalidenstrasse 43, German Democratic Republic; H. Schumann.
ZMU	Division of Entomology, Zoological Museum of the University, SF-00100 Helsinki

10, Finland; B. Lindeberg.

ZMUC Zoologisk Museum, Universitetsparken 15, DK 2100, Copenhagen, Denmark; S. Andersen.

2.2 Methods

2.2.1 Ranking of taxa

Ideally a classification should be practical to the general taxonomist, informative to the specialist, and an accurate reflection of the hypothesized cladistic relationships among included taxa. In reality few groups can be so perfectly classified, as the three criteria are often to a greater or lesser extent at odds with one another. The problem is particularly acute when cladistic relationships are inadequately known, as in the Siphonini. In light of this problem, and in an effort to adhere as closely as possible to the three criteria given above, a classification for the Siphonini is proposed using the formal supraspecific categories of genus and subgenus and informal category of species group, with different criteria for each.

The strictest criteria are applied to the category of genus. It is used here for monophyletic (holophyletic) lineages that are distinctly different morphologically from other such lineages. Most significantly, this has led to the broadening of *Siphona* to include a number of previously recognized genera (mostly of Townsend). This action has been necessary from a phylogenetic perspective to prevent the future erection of numerous new genera that would be necessitated by the yet undescribed, largely Neotropical, elements of this complex. This broadened concept of *Siphona* comprises a monophyletic group recognizable by the non-specialist. Lower ranks within the genus are used (as explained below) to serve the needs of the specialist.

The rank of subgenus has been used sparingly during the taxonomic history of the Tachinidae, particularly by the most prolific describer of New World tachinids, C.H.T. Townsend. Townsend had a very restricted generic concept, generally erecting new genera for the inclusion of one to several species. As Townsend's work is re-evaluated, most of his genera are being combined with others or his original generic limits expanded. With respect to the Siphonini, most of his genera proposed for non-*Siphona s.l.* species have been combined with other genera, leaving only his *Siphona* group genera, representing mostly New World taxa, unrevised. Whereas Townsend's genera now combined with non-*Siphona* genera required no change to the concepts of those taxa, the same is not true of his *Siphona* group names. Each of Townsend's names, with the exception of those now synonymized with *Siphona s.s.*, designate lineages of uncertain relationship to one another. Either they must all be retained as genera or the generic limits of another genus broadened for their inclusion. A compromise position has been adopted here by reducing Townsend's *Siphona* group genera to subgenera within a broadened concept of *Siphona*. *Siphona s.l.* is strictly monophyletic under this classificatory scheme, and the uncertain relationships of lower units are given the equal rank of subgenus to reflect the uncertain cladistic relationships among them. Thus such distinctive groups as *Baeomyia* and *Ceranthia* are also assigned subgeneric rank because their exclusion would make *Siphona s.l.* paraphyletic. By retaining Townsend's genera in a formal classification, albeit at lower rank, the information content of these taxa is retained, whereas it would be lost if *Siphona* was broadened and no lower ranks recognized.

All *Siphona* subgenera are considered strictly monophyletic except one. An exception has been made for *S. (Aphantorhaphopsis)* on practical grounds. Old World species of the *Siphona* group not belonging to *Siphona s.s.* or *S. (Ceranthia)* have been assembled together in *S. (Aphantorhaphopsis)* as a preliminary measure until the group can be adequately revised. Many of its described species are known only from holotypes - some male, others female - severely restricting their detailed study. Given also the rich undescribed fauna that similarly belongs within this group, a revision of this assemblage is not attempted within this work. Preliminary study of these species suggests they have few, if any, close relationships with New World *Siphona s.l.* species, and almost certainly no close relationships with the New World *Siphona* subgenera here recognized.

The lowest supraspecific rank used here is that of the informal species group. This rank is used for strictly monophyletic assemblages of species, and is used in two parts of the classification, once in *Ceromya s.l.* and again in *Siphona s.l.*

The species of *Ceromya s.l.* are arranged in *Ceromya s.s.* and the *C. silacea* species group, each thought to be monophyletic. This arrangement is presently both tentative and incomplete because each can only be recognized by examination of male genitalia and not all species of *Ceromya s.l.* were examined for male genitalic states. The two groups of *Ceromya s.l.* are referred to as above to reflect the tentative nature of these findings and to avoid premature changes to the classification. If future studies support the monophyly of each group and their sister group relationship then both ought to be formally recognized as subgenera of *Ceromya s.l.*

Nearly 100 undescribed siphonine species are known from the New World. More than half belong to such distinctive taxa as *Actia*, *Ceromya* and *Siphona s.s.*, or are included in the revised concepts of such *Siphona* subgenera as *Pseudosiphona* and *Siphonopsis*. The remainder do not exhibit clear relationships with any of the named taxa, although relationships are evident among some of these species. To reflect these relationships, document diversity, and to guide future studies on the assemblage, three numbered species groups are separately discussed, and the remaining 20-odd species treated as a whole. Thus the assemblage of known but undescribed species of New World *Siphona s.l.* is discussed in as detailed a manner as possible at this time. The naming of new species and possibly supraspecific taxa awaits a more detailed systematic examination of this diverse and undescribed fauna.

2.2.2 Treatment of undescribed species

No new species is described in this work, though the characteristics of many are incorporated into the descriptions of the supraspecific taxa. I consecutively numbered (according to country or region of origin) undescribed species within each supraspecific taxon so that information obtained from these undescribed species could be usefully expressed herein. The examined specimens were appropriately labelled to permit their recognition during future systematic studies of the Siphonini.

The numbering of undescribed species is inclusive of two or more higher taxa in two groups. The first involves *Ceromya s.l.*, in which undescribed species are numbered consecutively according to country or region of origin regardless of their placement in *Ceromya s.s.* or the *Ceromya silacea* species group. The second group involves species included in New World *Siphona* species groups 1 and 3 and unplaced species of New World *Siphona s.l.*: these were numbered as a whole consecutively from 1 to 34. Groups 1 and 3 were recognized after the original numbering system was adopted, so their numbers were not changed when the species were shifted to their present classification. (*Siphona* species group 2 was recognized before the other groups, and includes ten species numbered from one to ten.) One species from the above series, sp. 31, was recognized as near *S. (Uruactia) uruhuasi* and transferred to *S. (Uruactia)* without a change in number. Due to other taxonomic changes, no species in the *Siphona s.l.* series are numbered 9, 11 or 18 (*i.e.* these numbers are not used to designate undescribed species).

2.2.3 Terms

Terms used here are those proposed by McAlpine (1981), with several changes as discussed in O'Hara (1983a: 269-70). Two additional changes are made with respect to male genitalia because of conflicting theories about homology. Griffiths' (1972, 1981) interpretation of homologies in male genitalia differs from that of McAlpine (1981), so the neutral terms pregonite and postgonite here replace McAlpine's controversial homology of these structures with, respectively, the gonopod and paramere. I also use the common terms epandrium and surstylus, though for descriptive purposes only and not in rejection of Griffiths' periandrial hypothesis about development of these structures.

The male abdominal sternum 5 is a sclerite of varied shape among siphonines. There do not appear to be standard terms available for detailed description of this structure, so I have chosen arbitrary terms for this purpose, and explain their meaning in the Structural Features chapter in characters 38 to 40. Features of this structure are labelled in Fig. 47.

Many terms used for head features, thoracic and abdominal setation, and genitalic structures are labelled in figs. 1-12 in O'Hara (1983a: 345-8); wing veins are labelled here in Fig. 21, features of first instars in Figs. 157-158, and varied external and genitalic features are labelled on scanning electron photomicrographs, Figs. 23-46.

2.2.4 Examination and illustration of specimens

Adult specimens were examined with a Wild M5 stereoscopic microscope, with standard light source, at magnifications to 50X. Genitalia and first instars were studied with a Leitz SM-LUX compound microscope at magnifications to 400X. Though most genitalic features are visible at 50X with a dissecting microscope, there are certain taxonomically and phylogenetically important characters of the male genitalia, particularly those of the pregonite (characters 44-46), not readily discernable unless examined at 100X with a compound microscope or high resolution dissecting microscope (as discussed under appropriate characters in the Structural Features chapter).

Structures were drawn with the aid of a camera lucida or drawing tube, as explained in O'Hara (1983a: 268-9). Certain structures were gold-coated and examined and illustrated using a Cambridge M-250 scanning electron microscope. Illustrations referred to in other works are cited as "fig.", original illustrations shown in this work are cited as "Fig.".

2.2.5 Genitalic dissections

Male and female genitalia of siphonines provide some of the best character systems for taxonomic study and phylogenetic analysis. The genitalia of more than 600 siphonines were dissected during this study, following the method of O'Hara (1983a: 271-2). Briefly stated, this procedure involved removal of the abdomen from an adult specimen, partial clearing of the abdomen in 10% NaOH, dissection of genitalia, reattachment of abdomen to specimen, and storage of genitalia in glycerine. The abdomen generally changed little from its pre-dissection condition except for slight clearing and some shrivelling. Perhaps because of these minor changes, plus the time involved in preparation, most past workers have avoided study of siphonine genitalia despite the wealth of taxonomic and phylogenetic information they contain.

Genitalic preparations were stored during this study in short vials of glycerine in specially designed trays (O'Hara and McIntyre 1984), permitting direct examination and comparison among genitalia. Each dissection was numbered such that adult specimens and genitalia could be stored and examined separately and later easily re-associated. Genitalia were placed in microvials and pinned below their respective adult specimens for return of institutional loans. Dissection tags were placed in each microvial and attached to each pin to help prevent future accidental disassociation of genitalia and adult specimens, and to allow particular dissections referred to, or illustrated, herein to be identified and restudied.

Each dissection was color-coded and numbered. The following colors were used, and a one letter abbreviation of each color identifies the appropriate dissection series in the text: blue (B), green (G), orange (O), red (R), white (W) and yellow (Y).

2.2.6 Preparation of first instars

Adult female siphonines are larviparous, maturing eggs to the active first instar stage before oviposition. It is therefore possible to obtain first instars from dried specimens of mated adult females. Approximately 30% of the adult female specimens dissected during this study contained developed first instars, and these were prepared for examination and storage by the method described below.

The abdomen of an adult female siphonine was detached from the thorax and partially cleared in 10% NaOH. While still in the NaOH solution, the genitalia were dissected out and the abdominal cavity examined. Larvae, if present, were carefully teased from the abdomen and allowed to clear to a nearly transparent state. Genitalia and abdomen were then prepared as discussed above and in O'Hara (1983a: 271-2). Once larvae were sufficiently cleared, the NaOH solution was replaced with several washes of distilled water. Larvae were next transferred to a watch glass containing a 10% solution of glycerine. By allowing the water to slowly evaporate from the glycerine solution (usually requiring a couple of days), larvae generally absorbed glycerine at a slow enough rate to prevent collapse or distortion of their extremely delicate exoskeleton. Larvae were stored for study in glycerine in genitalia dishes along with the female genitalia, and later transferred to microvials when borrowed specimens were returned.

3. STRUCTURAL FEATURES

3.1 Historical review

The very long geniculate proboscis of *Siphona s.s.* species was recognized as a fundamental feature of that genus from the earliest writings about the Siphonini, but it was not until publication of Mesnil's work entitled "Genres *Actia* Robineau-Desvoidy et Voisins" (1954) that the concepts of other large siphonine genera reached their near-modern forms.

Mesnil (*op. cit.*) perceptively recognized the diagnostic value of two structural features of siphonines that had been noted by previous authors but not used at the generic level. One was Villeneuve's discovery (1924: 22) that the anal vein extended to the wing margin in certain species, which Mesnil used in the first couplet of his 1954 key (pp. 8-10) to distinguish *Strobliomyia* (=*Peribaea*), *Ceranthia*, *Siphona s.s.* and *Siphona (Asiphona)* (=*S. (Aphantorhaphopsis)*) from other siphonines. This state is now considered synapotypic of that group of taxa.

Mesnil (*op. cit.*) also recognized the generic value of Malloch's discovery (1930b: 120) that a group of species possesses a long, downwardly directed, lower proepimeral seta. Mesnil used this feature to differentiate *Strobliomyia* from other genera in which the anal vein is extended to the wing margin, and to separate what are now considered neaerine genera from other siphonines.

Mesnil (*op. cit.*) further distinguished between two groups of genera based on basal setulation of wing vein R_{4+5}. In one group R_{4+5} was setulose from base to crossvein *r-m* or beyond, in the other only a single setula was present basally. Within the former group Mesnil keyed out *Goniocera* and established the modern concepts of *Actia* (as *Entomophaga*) (based on the presence of a row of hairs on the katepisternum), and *Ceromya* (based on absence of this row of hairs). Mesnil's latter group was later transferred to the Neaerini by Herting (1957), based on study of female genitalia in the Calyptratae.

Mesnil synthesized the contribution of Herting (1957) into his revision of Palearctic tachinids in "Die Fliegen der palaearktischen Region" (1962-5). In that work Mesnil firmly established the modern concept of the Siphonini (as Siphonina), recognizing presence of a row of setulae on R_{4+5} as one of the fundamental features of the tribe. His generic classification, little changed from his 1954 publication, has become the touchstone of modern siphonine systematics.

Characterization of the Siphonini *sensu* Mesnil suffered from one shortcoming, namely the lack of a single feature which could be considered synapotypic of the tribe. Such was the situation when this work began in 1981. By then Crosskey had revised the siphonine fauna of all Old World non-Palearctic regions (1973, 1976a, 1980), but the siphonine fauna of the New World was essentially unrevised and the applicability of Mesnil's tribal concept to the Neotropical fauna, in particular, was untested. At the suggestion of D.M. Wood, Biosystematics Research Centre, Ottawa, I investigated the possibility of two spermathecae in the female reproductive system being synapotypic of the Siphonini. All dissections of females during this study suggests that this state is synapotypic, and the same conclusion was reached independently by Andersen (1983). This fundamental feature of adult female siphonines is here used to define the world Siphonini and supplement former external characterization of the tribe based on Old World members.

3.2 Structural features of the Siphonini

The two major revisions of the Siphonini are those of Mesnil (1962-5) and Andersen (1983). Both are primarily based on the Palearctic fauna, and hence do not provide detailed information about the distribution of character states throughout the tribe. Such information is desirable not only to provide a sound phylogenetic basis for supraspecific concepts and descriptions (and an accurate key), but also as an aid to future revisers of siphonine taxa. There follows an explanation of the characters used in the descriptions of the supraspecific taxa of the Siphonini, with designation of the states as they appear in Table 1. Table 1 is primarily intended as a quick reference to the distribution of character states within the Siphonini, both to summarize similarities and differences among supraspecific taxa and to augment the phylogenetic analyses of these taxa in the Evolution chapter.

Character 1. Length

Adult siphonines are relatively small tachinids, ranging in total length from 2.0-6.5mm (as measured in profile from apex of flagellomere 1 in resting position to apex of abdominal tergum 5), with most species averaging between 3.0-5.0mm. Like most tachinids, adult siphonines vary intraspecifically in size probably because of nutritional constraints placed upon them during their parasitic larval stage. It is thus not unusual to observe a considerable size range among conspecifics. This notwithstanding, the size of most individuals is closely grouped about the mean of that species, such that each species has a characteristic size. Ranges in total length given in Table 1 represent the size range observed among examined specimens of each taxon, and are rounded to the nearest 0.5mm.

Character 2. Proclinate orbital setae

Two proclinate orbital setae are present on each side of the vertex of both male and female siphonines. Two states are recognized, one in which the anterior seta is longer than the posterior one (A), the other in which both setae are subequal in length (S). This character is not always useful taxonomically since some species possess both states and in others males and females differ (with the anterior seta larger in the female than in male in these species). There is also no evident trend toward one state or the other among the major siphonine lineages. In addition to the two states recognized here there is also marked variation, though difficult to quantify, in length and thickness of the proclinate orbital setae (particularly the anterior one) among siphonine lineages.

Character 3. Frontal setae

Siphonines have a row of reclinate frontal setae which extend from about pedicel height to the anterior reclinate orbital seta. In all species except *Proceromyia pubioculata* the frontal setae alternate short and long, in *P. pubioculata* they are all long and unusually thin (Fig. 3). Also unique to *P. pubioculata* are 8-12 frontal setae, as other siphonines have no more than five (rarely six in atypical specimens). In many siphonines the fifth (uppermost) frontal is very short, and in few lost altogether (often intraspecifically varied); a few species among different lineages characteristically possess only three frontal setae, though a series of specimens is needed to determine the stability of this state. The number of frontal setae in each taxon is listed in Table 1, and an asterisk beside a five is used to indicate that three or four frontals occur in some species (either characteristically or as an aberration).

Character 4. Eye vestiture

As a rule siphonines have bare (B) eyes (*i.e.* only very few short and widely spaced hairs visible). The exception is *Proceromyia pubioculata*, which has a densely haired eye (D).

Character 5. Male eye height

Eye size is markedly varied among siphonines, and as such is one of the most useful external characters for species recognition. Variation among species renders this character of little value at the generic level. In some lineages males and females of a species are apparently very similar in eye size, in other lineages the male or female may have the larger eye; this distinction was difficult to document with accuracy because of interspecific variation and because both male and female specimens of a species were not always available for comparison, yet I have made generalizations in the generic descriptions based on specimens available. Male eye size was selected as the standard for comparison among genera because males generally vary more in eye size interspecifically and possess the better characters for species identification (*i.e.* features of the male genitalia).

Overall eye size is difficult to measure, so eye height is used here for comparisons. Eye height is taken as the maximum vertical distance from top of eye to bottom, relative to vertical head height (excluding ocellar triangle; as in O'Hara 1983a). Some authors (*e.g.* Andersen 1982) measure eye height on a diagonal axis, resulting in slightly greater values than given here. Ranges in eye height are recorded in Table 1 and in descriptions; as well qualitative differences are given in the latter as an aid for comparisons, according to this arbitrary guide: small, eye up to 0.65 head height; medium-small, 0.66-0.69; medium, 0.70-0.76; medium-large, 0.77-0.84; and large, 0.85 and greater.

Character 6. Male flagellomere 1 length

Characteristics of flagellomere 1, like eye size, are among the best external features by which to recognize species. One aspect that is easily quantified is that of flagellomere 1 length, as measured in profile from the suture on the pedicel to the most distant point apically, and expressed in relation to vertical head height (as in O'Hara 1983a). Male flagellomere 1 length has been used here for comparisons among genera because males of most species have the larger flagellomere 1 (*i.e.* longer and broader) and thus exhibit more interspecific variation in this character than females. As with eye height, a qualitative guide to flagellomere 1 length accompanies the numerical range given in descriptions, as an aid for comparisons among taxa. The following arbitrary length classes are used: short, less than 0.40 head height; medium-short, 0.41-0.48; medium, 0.49-0.60; medium-large, 0.61-0.69; and large, 0.70 and greater.

Character 7. Special modifications of male flagellomere 1

Though the majority of siphonines possess an average shaped flagellomere 1, males (and only males) of few species have unusual modifications, the functional significance of which is unknown. Included in this category are: bilobed flagellomere 1 (B; *e.g.* figs. 3a, 4a and 5a in Shima 1970a); trilobed flagellomere 1 (T; *e.g.* fig. 2a in Shima 1970a); and pectinate flagellomere 1 (P; *e.g.* Fig. 11, and fig. 1a in Shima 1970a). Absence of such modifications is indicated by an A in Table 1. The bilobed condition of male flagellomere 1 is found in other tachinids besides the Siphonini (*e.g.* some species of the neaerine genus *Phytomyptera* Rondani), and a similar type of pectinate flagellomere 1 is found in males of *Borgmeiermyia* Townsend (figs. 1-5 in Arnaud 1963).

Character 8. Shape of male flagellomere 1

Considered here is the general shape of male flagellomere 1, excluding the extreme modifications discussed under character 7. It is difficult to characterize flagellomere 1 shape into classes because its shape varies from one form to another in a continuous, non-graded manner. The following states are broadly defined to cover the range of observed variation in shape of male flagellomere 1, and the cited figures illustrate examples of each. The states are:

L, linear (Fig. 14); A, average (Fig. 17); B, broad (Fig. 6); S, subquadrangular (Fig. 15); and T, large and triangular.

Character 9. Aristomere 1 length

The majority of siphonines have a short aristomere 1 (S), with a length half or less that of its width. Aristomere 1 is slightly elongate (E) - subequal in length and width - in few species of several taxa. Most useful taxonomically and phylogenetically is state L (Figs. 4-5, 15), in which length of aristomere 1 is much greater than width (usually 2-4X longer than wide).

Character 10. Aristomere 2 length

Aristomere 2 is elongate, at least 1.5X longer than wide, with most siphonines having an aristomere 2 in the range of 2-4X longer than wide. Length of aristomere 2 varies markedly within genera, and to a lesser degree even within some species, so this character is of limited taxonomic value above the species level. As a generalization, species with a very large flagellomere 1 also possess a long aristomere 2, so there is some correlation in size between these structures in some lineages. Similarly, a long aristomere 2 generally accompanies a bilobed, trilobed or pectinate flagellomere 1. In Table 1 the range in size (length divided by width) of aristomere 2 is given for each taxon.

Character 11. Aristomere 3 length

Aristomere 3 is varied in overall length and also in the degree to which it is tapered along its length, with length, and thickness along length, generally correlated. For this reason I have taken a subjective approach to this character rather than a strictly numerical one, using states that are visually interpretable. However, the difference between one state and another in the following series is subtle and the cited figures should be referred to as a guide for their discrimination. The states are: V, very short and either evenly tapered to tip or thickened to near tip (Fig. 15); T, short and thickened to near tip (Fig. 8); S, rather short and usually evenly tapered to tip (Figs. 10, 16; a very subjective interpretation of an aristomere 3 intermediate in form between T and the next state); and L, long and evenly tapered to fine tip (most figures; *e.g.* Figs. 6, 12, 18). Clear differences in shape and length of aristomere 3 among some lineages are useful both taxonomically and phylogenetically, even though intermediate states are difficult to categorize.

Character 12. Arista vestiture

Amount of pubescence on the arista is constant within few lineages and greatly varied in most. Lack of apparent pubescence is referred to as almost bare (B; most figures, *e.g.* Figs. 14-16). Other states form a graded series from micropubescent (M; Figs. 7, 20), pubescent (P; Figs. 10, 17), short plumose (S; Fig. 13), to medium plumose (L, long). Refer to the cited figures as a guide to these states.

Character 13. Clypeus

The clypeus is visible as a small sclerotized structure above the maxillary palpi when the proboscis is at least slightly extended. It is varied in form from narrow and partially enclosed laterally in membrane (N), to slightly (S) or distinctly broadened (B), to U-shaped (U).

Character 14. Maxillary palpus

Most siphonines have a rather short, apically clavate palpus (S; most figures, *e.g.* Figs. 13-15). Particularly in species with an elongate proboscis, the palpus is correspondingly longer (L; Figs. 9, 20) and also apically clavate (*e.g. Siphona s.s.*). In *S. (Ceranthia)* species and two species of *S. (Aphantorhaphopsis)* the palpus is cylindrical (C; Fig. 16) along its length and varied in length from very short (reduced) to average.

Character 15. Prementum length

Almost all species with padlike labella have a short (S; *e.g.* Figs. 1-2, 5-6) to medium length (M; *e.g.* Figs. 14, 18) prementum (*prem*). Species with elongate labella almost always have an elongate prementum (E; Figs. 9, 20) as well. I have not classed these states into discrete sizes, but as an approximate guide short is less than half head height, elongate approximates or exceeds head height, and medium is intermediate.

Character 16. Labella

Of considerable taxonomic and phylogenetic importance is length of the labella (*lbl*). The groundplan condition is padlike labella (P; *e.g.* Figs. 1-8), and this state is widely distributed throughout the Siphonini. A state common to many lineages but independently derived within most of them are slightly lengthened labella (S), which are slightly longer than wide. Less common are the following states: M (Figs. 13, 17), labella moderately lengthened and subequal or slightly longer than half prementum length (characteristic of most *S. (Pseudosiphona)* species); E (Fig. 18), labella elongate and slightly shorter to longer than three-quarters prementum length (typical of most *S. (Siphonopsis)* species); and L (Figs. 9, 20), labella as long or longer than prementum (all *Siphona s.s.* species and few species in other lineages).

Character 17. Prosternum

The prosternum of most siphonine species is setulose (S), generally with a single pair of setulae but in few species with several pair. A bare prosternum (B) is characteristic of few species, though more commonly a bare specimen is found of a species in which the prosternum is generally setulose.

Character 18. Lower proepimeral seta

All siphonines have a strong, upturned seta (*u prepm s*) on the lower portion of the proepimeron. In addition, a strong lower seta (*l prepm s*) is present and directed downward in *Peribaea* (state P; Fig. 27). In other taxa the lower proepimeral seta (prostigmatic seta of some authors) is hair-like or absent (A; Fig. 28).

Character 19. Anepisternum

The upper region of the anepisternum has a patch of hairs and one to three larger setulae (*anepst s*), as recorded in Table 1 (one large setula shown in Fig. 32, two in Fig. 31). In most species the number of setulae is apparently constant, in others varied; as well certain genera have a characteristic number of setulae while in others the number is varied.

Character 20. Katepisternum anterior to mid coxa

The katepisternum is considered bare (B) anterior to the mid coxa if several hairs are present along (and restricted to) the lower portion adjacent to the ventral midline (Fig. 34). In most *Actia* species and *Entomophaga exoleta* a row of hairs (*kepst h*) extend upward anterior to the mid coxa from the ventral midline almost to the lower katepisternal seta (S; Fig. 33).

Character 21. Lower katepisternal seta

Three setae are in a triangular arrangement on the upper portion of the katepisternum. The lower seta (*l kepst s*) is varied in length, and compared with the upper anterior seta is shorter (S; Fig. 31), approximately equal in length (E), or distinctly longer (L; Fig. 32 [seta appearing equal in length to upper anterior seta due to perspective]).

Character 22. Postsutural dorsocentral setae

Three or four postsutural dorsocentral setae are present, as indicated in Table 1. As a generalization, the setae are longer and thicker (*i.e.* stronger) in species with three postsutural dorsocentrals than in those with four. Though the states of this character are very constant within some species and lineages, they vary within few species (*e.g.* several species of *Siphona s.s.*).

Character 23. Preapical anterodorsal seta on fore tibia

This seta is varied from apparently absent to long. As compared with the preapical dorsal (*d*) seta on the fore tibia, it is either shorter (S) or approximately equal in length or longer (E).

Character 24. Anterodorsal seta on mid tibia

Most siphonines possess one strong anterodorsal seta (*ad s*) on the lower half of the mid tibia (Fig. 37). This seta is lacking from *S. (Baeomyia)* species (Fig. 38) and several species of *Actia*, and a row of *ad* setae is present in *Goniocera*. Number of *ad* setae present on the mid tibia is shown in Table 1.

Character 25. Tarsomere modification

An average (A) tarsus is common to the groundplan of the Siphonini. One to several species in separate lineages possess a modification in tarsomere 5 of females (not known in males). Tarsomere 5 is enlarged in these species - broader and longer than in other siphonines (*e.g.* fig. 22 in Richter 1980 [female mislabelled as male]) and in most species with a dense patch of sensory hairs ventrally. This specialization is restricted to the fore leg in most species (F), but is present on all legs in very few (L).

Character 26. Tarsal claw length

Male and female claws and pulvilli are short in most siphonines (S; *e.g.* figs. 4 and 6 in O'Hara 1983a). In few species the claws are large (L; *e.g.* fig. 5, *op. cit.*), and generally larger in males than females. M designates a medium or intermediate-sized tarsal claw.

Character 27. Wing vein R_1 dorsally

Setulation of vein R_1 dorsally can be discretely divided into three states: B, bare (Fig. 22); D, setulose distally; and E, setulose along its entire length (Fig. 21). Species do not vary between states D and E, though many species vary between B and possessing one to several setulae distally near the costal margin.

Character 28. Wing vein R_1 ventrally

Vein R_1 ventrally is either bare (B) or distally setulose (D). As with character 27, some species vary between state B and possessing one to several setulae distally near the costal margin.

Character 29. Wing vein R_{4+5} dorsally

Setulation of vein R_{4+5} is the most useful wing character taxonomically other than character 33. It is setulose (with four to many setulae) in all siphonines and is one of the diagnostic features of the tribe. Two states are recognized, and only very few species vary between one state and the other: P (proximal), R_{4+5} setulose between base (bifurcation of R_{2+3} and R_{4+5}) and crossvein *r-m* (Fig. 22); and E, R_{4+5} setulose from base to beyond crossvein *r-m* (Fig. 21).

Character 30. Wing vein CuA_1 dorsally

Most siphonines have either a bare (B; Fig. 21) or partially setulose vein CuA_1. This vein is either setulose from crossvein *bm-cu* outward (S; Fig. 22), or in very few species is additionally setulose proximal to *bm-cu* (P). State P is constant in those species with that state, but a few species vary between state B and possessing several setulae on CuA_1 (a row of setulae on CuA_1 is a good species-constant state).

Character 31. Setulation of other wing veins

Setulation described in characters 27-30 are average for the Siphonini (A). Setulation on normally bare veins is noted here for several species: B, *Ceromya* Brazil sp. 5, with veins *Sc* and R_{2+3} setulose ventrally; C, *Actia ciligera*, with veins R_{2+3}, R_{4+5} and *M* setulose dorsally and ventrally; F, *Actia fallax*, with vein *M* setulose ventrally; M, *Peribaea modesta*, with vein R_{2+3} setulose dorsally and ventrally; and S, some specimens of the *S. (Actinocrocuta) singularis* complex, with vein *Sc* setulose ventrally.

Character 32. Loss of vein M distally

Veins are complete (C) in the majority of siphonines; in some species of *Actia* (involving several species groups) vein *M* fades out before its charcteristic bend towards wing tip in the apical one-fourth of wing (N). In few *Actia* species the bend of *M* is faint but still visible.

Character 33. Anal vein

This is one of the most significant characters in the Siphonini. The anal vein either fades out before the wing margin (N; Fig. 21) or is extended to the wing margin at least as a fold (E; Fig. 22). The latter state is extremely rare in other tachinids, and of great diagnostic and phylogenetic importance in the Siphonini.

Character 34. Position of crossvein dm-cu

The position of crossvein *dm-cu* is varied from near wing margin (Fig. 21) to relatively far removed from it (Fig. 22). A measure of *dm-cu* position was obtained by dividing the distal length of CuA_1 (distance from *dm-cu* to wing margin) by proximal length of CuA_1 (distance from crossvein *bm-cu* to *dm-cu*). The range in values for each taxon is given in Table 1 along with the number of species examined (generally one specimen measured per species), the mean, and standard deviation (SD). This character is discussed in detail in the Evolution chapter.

Character 35. Median marginal setae on abdominal terga 1+2

Median marginal setae are considered absent (A) from abdominal terga 1+2 (T_{1+2}) if they cannot be distinguished from adjacent setulae. If they are slightly longer and thicker than adjacent setulae then they are considered weak (W), and if subequal in size to the median and lateral marginals on T_3 they are strong (S) (states A and S are illustrated in figs. 7-8, O'Hara 1983a). Some species with state S are very constant for this state, while in other species all states are present among different individuals, or some specimens have a strong median marginal on one side and lack one on the other.

Character 36. Lateral marginal setae on abdominal terga 1+2

States A (absent), W (weak) and S (strong) are the same as described for character 35 (see figs. 7-8 in O'Hara 1983a for states W and S). This character varies intraspecifically as in character 35, though generally such variation is between states A and W; most species with strong lateral marginal setae (S) rarely vary from this state.

Character 37. Setation on abdominal terga 3 to 5

The average condition (A) is one in which tergum 3 (T_3) has a pair of strong median and lateral marginal setae and tergum 4 (T_4) and tergum 5 (T_5) each with an evenly spaced row of six marginal setae (figs. 7-8 in O'Hara 1983a). Additionally, in some species T_3-T_5 possess weak to strong lateral discal setae (D) and/or an extra pair of lateral marginal setae (L).

Character 38. Posterior processes of male abdominal sternum 5

Male sternum 5 (S_5) consists of an anterior (basal) plate (*bs p*) and two posterior processes. The processes are separated from one another by a median cleft (*med c*) and bordered anteromedially by a broad desclerotized area (*descl a*) of varied size (Fig. 47). Shape of the processes is greatly varied, but two general areas are recognized on each process: the apical lobe (*ap l*) and median lobe (*med l*) (Fig. 47). In most *Actia* species the median lobes are undifferentiated and the apical lobes are long and broadly continuous with the processes, resulting in a more or less V-shaped S_5 (A, *Actia*-type; Figs. 58-59). In a few other siphonines S_5 resembles the A state of *Actia* except the median lobes are distinctly differentiated and partially enclose the median cleft (V; Figs. 61, 64). In most siphonines the apical lobe is more narrowed preapically, and in combination with a distinctly differentiated median lobe produces a sharply or broadly defined U-shaped posterior margin (U; *e.g.* Figs. 47, 50, 65-70) or one in which the angle between apical and median lobes is obtusely angled (O; *i.e.* an intermediate state between V-shaped and U-shaped, *e.g.* Figs. 48-49, 60). A few siphonines have an undifferentiated apical lobe and rounded median lobe, producing a more or less transverse sternal margin posteriorly (T; Figs. 51-52, 57).

Character 39. Apical lobe of male abdominal sternum 5

Within lineages possessing a preapically narrowed apical lobe and U-shaped S_5 posteriorly (see character 38), there is a trend toward curving inward (*i.e.* medially) of the apex of the apical lobe. State A designates the average condition in which the apical lobe is directed posteriorly (*e.g.* Figs. 47, 50, 66-68); C, an apical lobe distinctly curved inward (Figs. 56, 62-63, 65, 69); and S, an intermediate state in which apical lobe is slightly curved inward (Figs. 53-54).

Character 40. Median lobe of male abdominal sternum 5

This feature of considerable variation is here defined as the region bordering the median cleft posteriorly, and continuous with the posterior process laterally. It is undifferentiated (U) in those species of *Actia* in which the sternal margin posteriorly is

V-shaped and median cleft not bordered by lobes (Fig. 58). In the simplest developed form the median lobe is rounded along its median margin (R) and partially encloses the median cleft (*e.g.* Figs. 55, 64, 67). In more developed forms the median lobe is truncate (T; *e.g.* Figs. 63, 66) along its medial or posteromedial margin or very broad and longitudinally elongate (E; *e.g.* Figs. 53, 69). In *Goniocera* species and a few other species the median lobe forms a broad, truncated plate flattened in a more or less posteromedial plane (F; Figs. 47, 54). State F is a highly derived form of median lobe, and between it and state T are a range of intermediates here classed as state I, characterized by a truncate margin and rather flattened surface posteromedially (Fig. 68). Some species, particularly within *Siphona s.l.*, have an accessory lobe on the median lobe posteriorly (A; Fig. 70).

Character 41. Setulation of male abdominal sternum 5

Sternum 5 is bare on the basal plate, anterior to the desclerotized area. The posterior processes are sparsely (S), moderately (M), or densely (D) setulose. The processes may also have one pair of setae distinctly larger than the surrounding setulae, but presence or absence of these setae has been interpreted as too intraspecifically varied to be usefully characterized here.

Character 42. Size of male abdominal tergum 6

Male tergum 6 (T_6) is separated from the epandrium by a narrow strip of membrane. In a few siphonines T_6 is unsclerotized (A, apparently absent), while in most it is varied from tiny to small lateral sclerites (S), to larger lateral sclerites (L), to a narrow to broad dorsally continuous sclerite (D).

Character 43. Width of ejaculatory apodeme

The ejaculatory apodeme in the male genitalia has a bulbous base and a fan-shaped apical portion of varied size. Width of the fan-shaped portion is expressed herein as a function of the preapical width of the hypandrial apodeme (as measured dorsally). The relative width of the fan-shaped portion is given either as a measured range or expressed in relative terms in Table 1 and descriptions. The following states of the latter are recognized:

N, ejaculatory apodeme slightly narrower than hypandrial apodeme; S, apodemes subequal in width; and W, ejaculatory apodeme slightly wider than hypandrial apodeme.

Character 44. Shape of pregonite

Pregonites are structures to either side of the aedeagus, articulated at their bases with the hypandrium. A thin membrane extends anteriorly from the apex of each pregonite to the ventral surface of hypandrium. Pregonite shape is varied in many and subtle ways and cannot be classified into states without grouping similar forms in a subjective manner. I have tried to select and describe states that I perceive as most meaningful in a taxonomic and phylogenetic sense, though it must be noted that even a continuous transformation series cannot be hypothesized since most states could easily have been derived from one of several others. The following states are recognized, and are arranged alphabetically because of the complexity of this character: A, average, smoothly curved along posterior margin or bent rather sharply at midlength, and pointed or rounded apically (Figs. 73-76, 89-94, 96-106); C, C-shaped (open side facing anteriorly) and broad at midlength (Figs. 87-88); F, fused basally with hypandrial apodeme (only observed in *S. (Aphantorhaphopsis) nigronitens*); J, broad subapically and more or less J-shaped (Figs. 85-86); L, linear and only slightly curved apically (Fig. 72); M, anterior membranous portion enlarged, apex of pregonite generally not curved anteriorly (Figs. 77, 79-81); O, ring-shaped, though part of ring incomplete in few species (Fig. 78); P, elongate and curved posteriorly (unique to *Ceromya lutea*, Fig. 83); S, thin and sickle-like, with basal arm slightly extended anteriorly (Fig. 84); T, basally broad and apically truncate (Fig. 71); and W, broadened or wide along most of length, with short pointed apex (Fig. 95).

Character 45. Pregonite modifications

The pregonite has a smooth outer surface in the groundplan condition. Spines (*sp*) or spinules (*spin*) adorn the pregonite in a number of genera, and the size, pattern and location of these are classed into discrete, non-continuous states. However, not all of the following states can be seen with a dissecting microscope (at 50X), so it is necessary to examine the pregonite at a power of 100X or more with a compound microscope to discern with certainty whether small spinules are present or absent (A; *e.g.* Figs. 72, 76, 84, 87-88, 90-94). The spinose states are: L, longitudinal ridge on anterolateral surface with spines in single row along edge (Figs. 73-75, 103-105); M, anterior membranous portion (*memb p*) of pregonite expanded, usually with field of spinules on lower portion (Figs. 39-40, 71, 83, 79-81; these spinules are too small to be seen with most dissecting microscopes in specimens of most species); E, similar to state M, but in addition has laterally directed spines on anterolateral portion of sclerotized area (Fig. 82); R, ring-shaped pregonite (state O in character 44) with spinules anteriorly (Fig. 78); S, sclerotized portion (*scl p*) of pregonite with field of spines distally, with largest spines along apical margin (Figs. 41-42, 85-86); and T, sclerotized portion of pregonite with field of tiny spinules distally (Figs. 89, 95, 100; as with state M, these spinules are very small in specimens of some species, and not readily discernible with most dissecting microscopes).

Character 46. Posterior seta on pregonite

Some members of *Siphona s.l.* possess a tiny to long seta at about midlength on the posterior surface of the pregonite. Different setal size classes are recognized because certain lineages possess a seta with a characteristic length. However, setal length is varied among some species, and varied between absent and small to medium in few. Given the varied nature of this character, the following imprecisely specified states are recognized: A, absent (*e.g.* Figs. 71-82); T, very tiny seta (Figs. 89, 93, 97-98, 103-104, 106; not readily discernable without aid of a compound microscope); M, short to medium-sized seta (Figs. 90-92); L, long, thick seta (Fig. 94; as characteristically present in species of *S. (Ceranthia)*); and F, two to few tiny to short setae (Fig. 95).

Character 47. Epiphallus

An epiphallus is a subbasal, posterior outgrowth of the aedeagus. A small epiphallus is best seen in dorsal or ventral view, where unobstructed by epandrium or postgonite. The following states are recognized: A, absent; S, small (short); N, relatively large but narrow; and P (present), relatively large and average width.

Character 48. Posterior margin of distiphallus

The distiphallus is a cylindrical structure of varied ~~size~~, shape and sclerotization. Several characteristics of the distiphallus appear to be more or less independent of one another, and three are considered here as characters 48 to 50. Character 48 describes the relative amount of sclerotization along the posterior margin of the distiphallus. The posterior margin is either entirely sclerotized to near apical margin of distiphallus (E), or is incised or desclerotized to varied degrees (I). The latter state can be recognized in lateral view in most species of *Siphona s.l.* by the presence of a pointed, sclerotized arm protruding from the distiphallus posteriorly, below the narrowed attachment of basiphallus and distiphallus.

Character 49. Posterolateral margin of distiphallus

The lateral surfaces of the distiphallus, as viewed in profile, provide among the best features for species separation and recognition within the Siphonini. Shape of the distiphallus is too varied to be fully categorized at the generic level, but two aspects have been selected for description as characters 49 and 50. Character 49 refers to the posterolateral margin (apically) of the distiphallus. In some siphonines it is reduced or not differentiated (*i.e.* not incised) from the rest of the distiphallus (A; *e.g.* Figs. 108-111, 115-124). In other siphonines the posterolateral margin of the distiphallus is incised from the rest of the lateral margin and slightly to markedly elongate, mostly independently among different lineages. This is a difficult character to classify into states, though the following series gives a rough indication of the diversity of this character among the recognized siphonine lineages: S, posterolateral margin separated from lateral margin by narrow incision and not extended beyond apex of lateral margin (present in *Goniocera io*, but not visible in Fig. 107 because posterolateral margins are curved inward); M, moderate apical extension of posterolateral margin beyond lateral margin and usually pointed or spined (either continuous with lateral margin or incised from it; Figs. 125, 131, 134); and E, as in state M but apically extended well beyond apex of distiphallus (Figs. 112, 114, 127, 133, 136).

Character 50. Spines on lateral margin of distiphallus

The lateral and anterolateral surfaces of the distiphallus are adorned with small spinules, especially conspicuous anteriorly and apically. In some siphonines no larger spines are present (A; Figs. 107, 115-118, 132-135), in others the lateral margins are armed with conspicuously larger, usually recurved, spines along anterior and/or apical margin (P; Figs. 108-111, 114, 121, 124, 128). The degree to which these spines are differentiated is very useful taxonomically, particularly at the species level, but is too varied to be categorized here.

Character 51. Postgonite size

Paired postgonites extend posteriorly from either side of the aedeagus basally. They are large (W, well developed) and conspicuous in most siphonines. Postgonites are short (S) in some siphonines (about as long as width of basiphallus subbasally), or reduced (R) to scarcely discernible lobes at base of basiphallus.

Character 52. Surstylus basally

The surstylus articulates basally with the epandrium and cerci. In most siphonines it is attached membranously (M; Figs. 139-144), in few there is a narrow sclerotized connection between the epandrium posteriorly and surstylus basally (F, epandrium and surstylus fused; Figs. 137-138).

Character 53. Shape of surstylus

The average condition (A) of the surstylus, as viewed in profile, is one in which it is narrowed at about midlength and either straight or slightly curved posteriorly near apex (Fig. 141). The following states are qualitative departures from the average condition (see cited figures for examples): S, short (Fig. 142); B, distinctly broader than average (Fig. 138); C, markedly curved posteriorly (Fig. 139); and L, elongate (Fig. 137).

Character 54. Shape of male cerci

The cerci of siphonines are fused medially and tapered to a single slender apex. Their shape is described in lateral view, with average (A) being slender on lower half, smoothly curved at midlength and curved anteriorly near apex (Fig. 141). The following recognized shapes are relative to the average shape: S, short (Fig. 138); B, broadened; E, elongate (Fig. 140); L, linear or straight along posterior margin in profile; R, same as state L but short (Fig. 139); and I, sharply inflexed at midlength, short to long in length (Figs. 137-138, 140; state I may be accompanied by one of the former states).

Character 55. Female ovipositor length

The ovipositor, or female genitalia, is primitively short and only slightly extensible. More extensible ovipositors have evolved independently within different lineages, perhaps as an adaptation for depositing larvae directly upon hosts (as suggested by Andersen 1983). Extensible ovipositors are telescopic and characterized by broad regions of intersegmental membrane, and often elongated sclerites as well. Degree of extensibility is classed as follows: S, short and only slightly extensible (Figs. 43-46, 146-148, 151-153); M, moderately extensible (Figs. 145, 149-150, 154); E, elongate (Fig. 155); and V, very elongate (Fig. 156).

Character 56. Shape of female sternum 6

The most apparent modifications to the female genitalia, other than extensibility, involve the shapes of sterna 6 (S_6) and 7 (S_7). Modification of S_6 is not common among siphonines, and is apparently always accompanied by similar or more pronounced modification of S_7. In the average (A) condition S_6 is slightly rounded on its ventral surface (Figs. 43-46, 145-153). Several types of modification are recognized: W, weakly or slightly keeled (*kl*) posteromedially; S, sharply keeled posteromedially (Fig. 154); M, moderately elongate (Figs. 154, 156); and E, elongate (Fig. 155).

Character 57. Size of female tergum 6

Female tergum 6 (T_6) is varied in size as follows: A, absent; S, very small lateral sclerites (Fig. 152); L, moderate-sized lateral sclerites (Figs. 145, 148, 151, 155-156); M, dorsomedian sclerite, not extended laterally; D, single sclerite extended dorsally and laterally (Figs. 153-154); and N, as in state D but narrowly discontinuous dorsally (Figs. 146-147, 149-150).

Character 58. Anterior apodeme on female sternum 7

Female sternum 7 (S_7) is without an anterior apodeme (A, absent) if its anterior margin is broadly rounded (Figs. 145, 149, 151-156). An apodeme is present if a sclerotized arm extends anteriorly from the anteromedian margin of S_7, and is classed as either short (S; Fig. 150) or long (W, well developed; Figs. 146-148).

Character 59. Shape of female sternum 7

As mentioned under character 56, modifications to sterna 6 (S_6) and 7 (S_7) are the most conspicuous in female genitalia other than extensibility. The following states are similar to those given for character 56: A, average condition, S_7 slightly rounded ventrally (Figs. 43, 45, 145-146, 148-153); W, weakly or slightly keeled (*kl*) posteromedially (Fig. 147); S, sharply keeled posteromedially (Figs. 44, 46); E, elongate (Figs. 155-156); and L, elongate and keeled posteromedially (Fig. 154).

Character 60. Size of female tergum 7

Female tergum 7 (T_7) is varied in size as follows: A, absent; S, very small lateral sclerites (Figs. 151-152) L, moderate-sized lateral sclerites (Figs. 145-150, 153); and F, lateral sclerites fused with S_7 (Figs. 154-156).

Character 61. Location of spiracle of segment 7

The position of the spiracle of segment 7 is varied. In some siphonines it is located in segment 7, close to or in T_7 or dorsal to margin of S_7 (state P, posterior; Figs. 148, 153-156). In other siphonines the spiracle is located dorsolaterally in membrane between segments 6 and 7 (state I, intermediate; Figs. 145, 150-152) or anteriorly in segment 6 in or near T_6 (state A, anterior; Figs. 146-147, 149).

Character 62. Characteristics of female sternum 8

Female sternum 8 (S_8) is varied in several ways. In the average (A) condition it is a small sclerotized plate partially covered by S_7, and sparsely haired posteriorly (Figs. 43-46, 146, 148-153; average condition but bare in *Peribaea* species). Other states are as follows: L, lacking or absent (Figs. 147, 154-156); **R**, reduced in size (Fig. 145); **W**, much wider than average; **B**, bare or almost so; and **S**, with thick setae posteriorly (setation not shown in figures).

Character 63. Size of female tergum 10

Tergum 10 (T_{10}) is located dorsal to the cerci (*cer*). It is small and sparsely haired in most siphonines, and present as either a median sclerite (**M**) or as two slightly separated sclerites (**P**, paired; a few species possess both states). In few siphonines T_{10} is unsclerotized (**A**, absent) or reduced in size (**R**).

Character 64. Labrum of first instar

The anterior end of the cephalopharyngeal skeleton of first instars of the Tachinidae is extended forward between the lateral sclerites, and is tentatively homologized with the labrum by Wood (1987: 1196) (often termed "mouth hook" by previous authors). As in other tachinids, the labrum of first instar siphonines varies from hook-like (**N**, narrow dorso-ventrally in profile; Figs. 160, 172-174, 189-191, 193) to hatchet-like (**B**, broadened dorso-ventrally in profile; Figs. 158, 161-164, 166-171, 176-187, 194-209). In few siphonines the labrum is intermediate between these states, and here termed slightly broadened (**I**; Figs. 159, 165, 175, 188, 192).

Character 65. Dorsal cornu of cephalopharyngeal skeleton of first instars

In most larval siphonines and other larval tachinids there are two cornua posteriorly on the cephalopharyngeal skeleton, one dorsal (*d corn*) and one ventral (*v corn*) (**P**; Figs. 158-167, 172-209). The dorsal cornu is absent (**A**) from all eight *Actia* species examined for this character (Figs. 168-171).

Character 66. Posteroventral margin of abdominal segment 7 of first instars

First instars of the Siphonini are equipped with spinules or spines externally. The greatest modification and variation in these structures are found on the last several abdominal segments, particularly the posteroventral margin of segments 7 and 8. Segment 7 is bare or has small spinules (B) posteroventrally (Figs. 157-163, 165-175, 180), or large spinules to hooks. If large spinules, spines or hooks are present (Figs. 164, 176-179, 181-209), their number is entered in Table 1 and descriptions.

Character 67. Posteroventral margin of abdominal segment 8 of first instars

Segment 8 possesses ventrally a row or rows of spinules or spines along its posterior margin, anterior to the anus. Two states are recognized: **R**, two or more even or uneven rows of spinules or spines (Figs. 157-161, 165-167, 170-175, 188-191); and **S**, a single dominant row of spinules or spines (Figs. 162-164, 168-169, 176-187, 192-209).

Table 1. Distribution of character states in the Siphonini. Refer to text for explanation of characters and states. (Superscripts indicate the number of species possessing a state, an asterisk denotes a state shared by most species in a taxon, an arrow signifies the presence of states intermediate to those on either side of arrow, and a diagonal slash (/) indicates that two states are present in the single examined species of that taxon.)

Character	1	2	3	4	5	6	7	8	9	10	11	12
	Length	Proclinate	Frontal	Eye	Eye	Male flagellomere one			Aristomere length			Arista
Taxon	(mm)	orbitals	setae	vestiture	height	length	modification	shape	1	2	3	vestiture
Goniocera	4.0-6.0	A,S^*	5^*	B	0.58-0.71	0.42-0.67	A	L,A,B	S	2-4	S,L	B,M
Proceromyia	3.0-5.5	S	5,8-12	B^1,D^1	0.78-0.84	0.34-0.43	A	A	S	1.5-3	S,L	B
Entomophaga	3.0-5.0	A,S	5^*	B	0.63-0.77	0.58-0.66	A	B,S	L	3-4	S	B
Ceromya s.s.	3.0-6.0	A^*,S	5^*	B	0.68-0.86	0.38-0.80	A^*,B^3	L→S	S	1.5-10	T→L	B→S
Ceromya silacea group	3.0-5.5	A	5^*	B	0.77-0.86	0.47-0.56	A	L→T	S	1.5-5	S,L	M,P
Actia	2.5-6.0	A^*,S	5^*	B	0.65-0.89	0.43-0.75	A^*,B^2	L,A,B	S	1.5-5	T→L	B→S
Peribaea	2.5-5.0	A^*,S	5^*	B	0.73-0.86	0.39-0.75	A^*,B^7,T^2,P^3	L,A,B	S	1.5-12	T→L^*	B→S,M
Siphona sensu lato												
S. (Actinocrocuta)	3.5-4.5	A	5^*	B	0.76-0.81	0.41-0.52	A	A	S	1.5	L	P,S
S. (Aphantorhapha)	2.0-3.5	A,S	5^*	B	0.71-0.83	0.43-0.54	A	L,A,B	S	2-4	T→L	M→S
S. (Aphantorhaphopsis)	3.0-5.0	A,S	5^*	B	0.69-0.89	0.38-0.63	A	L→S	S	1.5-4	T→L^*	B→S
S. (Baeomyia)	2.0-3.0	S	5^*	B	0.65-0.83	0.39-0.56	A	A,B,S	L	2-5	V	B
S. (Ceranthia)	3.0-5.5	A,S^*	5^*	B	0.69-0.88	0.42-0.66	A	B,S	S	2-8	S	B,M
S. (Pseudosiphona)	2.0-5.0	A,S	5^*	B	0.73-0.86	0.38-0.48	A	L→S	S,E^1	1.5-2	T→L	M→L
S. (Siphona)	2.5-6.5	A,S	5^*	B	0.62-0.91	0.40-0.75	A	L→T	S^*,E,L	2-10	T→L^*	B,M
S. (Siphonopsis)	2.5-4.5	A,S	5^*	B	0.73-0.84	0.37-0.65	A	A→T	S,E^2	1.5-6	T→L	B→S
S. (Uruactia)	4.0-5.0	A	5^*	B	0.84	0.48-0.50	A	A,B	S	2	L	M
Siphona s.l., sp. grp. 1	3.0-5.0	A,S^1	5^*	B	0.67-0.83	0.45-0.67	A	L→T	S,E^3	2-8	T→L	M,P
Siphona s.l., sp. grp. 2	2.5-4.5	A^*,S	5^*	B	0.78-0.86	0.42-0.54	A	L→S	S	1.5-3	S,L^*	M→S
Siphona s.l., sp. grp. 3	3.0-4.0	A	5^*	B	0.75-0.82	0.43-0.71	A	L→T	S	2-5	T→L	M,P
Siphona s.l., unplaced	3.0-5.0	A^*,S	5^*	B	0.69-0.91	0.39-0.55	A	L→T	S	1.5-4	T→L	M→S

Table 1 (cont.). Distribution of character states in the Siphonini.

Character	13	14	15	16	17	18	19	20	21	22	23	24
Taxon	Clypeus shape	Palpus shape	Prementum length	Labella shape	Prosternal setation	Proepimeral seta	Anepisternal setation	Katepisternum mid coxa	setae	Postsutural dorsocentrals	ad seta fore tibia	ad seta mid tibia
Goniocera	U	S	S	P	B,S	A	$0^2,1^1$	B	S	$3,4^1$	S^2,E^2	2-7
Proceromyia	U^1	S	S	P	B	A	$1^1,3^1$	B	S	3	E	1
Entomophaga	U	L	S	P	S	A	1	B^1,S^1	S	$3^1,4^1$	E	1
Ceromya s.s.	$N \rightarrow U^{\bullet}$	$S^{\bullet},L$	S	P,S^1	$B^1,S^{\bullet}$	A	$0^1,1$	B	S,E^2	3,4	S,E^3	$0^3,1$
Ceromya silacea group	U	S	S	P	S	A	1	B	S,E^3	3,4	S	1
Actia	$N \rightarrow U$	$S^{\bullet},L$	$S^{\bullet} \rightarrow E$	$P^{\bullet} \rightarrow L$	B^1,S	A	$1^2,2$	$B,S^{\bullet}$	S	$3,4^{\bullet}$	$S^{\bullet},E$	$0^4,1$
Peribaea	$S,U^{\bullet}$	S	$S^{\bullet},M$	P	S	P	$1^{\bullet},2$	B	$S \rightarrow L$	4	S	1
Siphona sensu lato												
S. (Actinocrocuta)	N,S	S	S,M	$P \rightarrow M$	S	A	1	B	L	3	S	1
S. (Aphantorhapha)	N,S	S	S,M	P,S^1	S	A	1	B	E,L	3	S	1
S. (Aphantorhaphopsis)	$N \rightarrow U$	$S^{\bullet},L,C^3$	$S^{\bullet} \rightarrow E$	$P^{\bullet} \rightarrow L$	B^1,S	A	$1^{\bullet},2$	B	E,L	3,4	S,E^1	$1,2^2$
S. (Baeomyia)	U	S	S	P	B,S	A	1	B	S,E	3	S	0
S. (Ceranthia)	$N \rightarrow U$	C	S	P	S	A	$1^{\bullet},2$	B	L	3,4	S	1
S. (Pseudosiphona)	N,S	S	$S,M^{\bullet},E$	$S \rightarrow L,M^{\bullet}$	S	A	1,2	B	E,L	3	S	1
S. (Siphona)	N	L	E	L	$B,S^{\bullet}$	A	$1^{\bullet},2$	B	$E,L^{\bullet}$	3,4	S	1
S. (Siphonopsis)	N	S	S,M	E	S	A	1	B	L	3	S	1
S. (Uruactia)	N^1,S^1	S	M	P	S	A	1,2	B	L	$3^1,4^1$	S	1
Siphona s.l., sp. grp. 1	N	$S^{\bullet},L$	$M^{\bullet} \rightarrow E$	$P \rightarrow E^{\bullet}$	S	A	$1,2^1$	B	L	$3,4^2$	S	1
Siphona s.l., sp. grp. 2	$N^{\bullet},S$	S	S,M	P,E^1	S	A	1	B	L	3	S	1
Siphona s.l., sp. grp. 3	N	S	S,M	P,S^1	S	A	$1,2^1$	B	L	3	S	1
Siphona s.l., unplaced	$N^{\bullet} \rightarrow U$	$S^{\bullet},L$	$S^{\bullet} \rightarrow E$	$P^{\bullet},S,L^2$	B^1,S	A	$1^{\bullet},2$	B	$S,E,L^{\bullet}$	$3^{\bullet},4$	S	1

Table 1 (cont.). Distribution of character states in the Siphonini.

Character	25	26	27	28	29	30	31	32	33	34			
	Tarsomere modification	Claw length	Vein R$_1$		R$_{4+5}$	CuA$_1$	Other	Loss of	Anal	Position of crossvein dm-cu			
Taxon			dorsally	ventrally	dorsally	dorsally	veins	vein M	vein	spp.	range	mean	SD
Goniocera	A	S,M	B	B	E	B	A	C	N	4	0.26-0.47	0.34	0.08
Proceromyia	A	L	B	B	P	B	A	C	N	2	0.24-0.32	0.27	0.03
Entomophaga	A	S^1,M^1	B	B	P	B	A	C	N	2	0.25-0.43	0.33	0.07
Ceromya s.s.	A$^\bullet$,F,L^1	S$^\bullet$,M	B,D,E	B,D	[illegible],E$^\bullet$	B,S,P^4	A,B	C	N	39	0.24-0.67	0.40	0.10
Ceromya silacea group	A	S	B,D,E	B,D	E	B,S	A	C	N	5	0.29-0.47	0.36	0.08
Actia	A$^\bullet$,F,L^1	S	B,D,E	B,D	P,E	B,S	A,C,F	N,C$^\bullet$	N,E^3	56	0.25-1.6	0.56	0.27
Peribaea	A,F^2	S,M$^\bullet$	B,D,E	B,D	E	B$^\bullet$,S	A,M	C	E	31	0.63-1.3	0.84	0.18
Siphona sensu lato													
S. (Actinocrocuta)	A	S	D,E	B	E	B,S	A,S	C	E	2	0.35-0.49	0.42	0.06
S. (Aphantorhapha)	A	S	B,E	B,D	P,E	B	A	C	E	6	0.44-0.85	0.64	0.13
S. (Aphantorhaphopsis)	A	S	B,D	B$^\bullet$,D	P,E^1	B	A	C	E	29	0.26-1.4	0.47	0.23
S. (Baeomyia)	A	S	B,D	B	P	B	A	C	E	5	0.64-1.0	0.85	0.09
S. (Ceranthia)	A	S	B$^\bullet$,D	B,D^1	P,E^1	B	A	C	E	19	0.30-0.51	0.42	0.07
S. (Pseudosiphona)	A	S	B,D,E	B	P,E	B	A	C	E	20	0.36-0.74	0.60	0.10
S. (Siphona)	A$^\bullet$,F	S$^\bullet$→L	B$^\bullet$,D,E	B$^\bullet$,D	P$^\bullet$,E	B$^\bullet$,S	A	C	E	71	0.26-0.67	0.41	0.07
S. (Siphonopsis)	A	S	B,D	B	P	B	A	C	E	16	0.29-0.55	0.43	0.07
S. (Uruactia)	A	S	D	B	P^1,E^1	B	A	C	E	2	0.26-0.46	0.36	—
Siphona s.l., sp. grp. 1	A	S,M^1	B,D	B	P,E^1	B	A	C	E	9	0.21-0.66	0.35	0.14
Siphona s.l., sp. grp. 2	A	S	B^1,D,E	B,D^1	P^1,E	B,S	A	C	E	10	0.26-0.67	0.51	0.11
Siphona s.l., sp. grp. 3	A	S	B,E^1	B,D^1	P,E	B,S^1	A	C	E	5	0.37-0.68	0.47	0.09
Siphona s.l., unplaced	A	S	B,D,E^1	B,D^1	P,E	B	A	C	E	17	0.22-0.86	0.45	0.15

Table 1 (cont.). Distribution of character states in the Siphonini.

Character	35	36	37	38	39	40	41	42	43	44	45	46
	Abdominal T_{1+2}		T_3-T_5		Male sternum 5			Size of	Ejaculatory		Male pregonite	
Taxon	m. marg.	l. marg.	setation	processes	ap. lobe	med. lobe	Setulation	male T_6	apodeme	shape	modification	seta
Goniocera	A→S	A→S	A,D	U	A	F	M	D	S,W	L,T^{1}	A,M^{1}	A
Proceromyia	A	S	A,D	O	A	R	M	D	W-1.5	A	L	A
Entomophaga	A	S	A,D	U^{1},T^{1}	A	R	M	D	W-2.0	A	A^{1},L^{1}	A
Ceromya s.s.	A	A→S	A*,D,L	O,U,T	A*,S,C^{1}	R,E,I,F,A	S,M	S→D	0.5-1.5	M*,O,P^{1}	M*,E,R	A
Ceromya silacea group	A	A→S	A,D	O,T	A	R,I^{1}	S*→D	S	0.5-S	A^{1},S	A	A
Actia	A	A*→S	A*,D	A*,V,O	A	U*,R,E	M	L→D	0.5-2.0,S*	J	S	A
Peribaea	A	A*→S	A*,D^{1},L	V,O,T	A	R*,E,I	M	S→D	S→W*	C	A	A
Siphona sensu lato												
S. (Actinocrocuta)	A	A,W	A	U	A→C	R	M	?A	S-2.0	A	T	A,T
S. (Aphantorhapha)	A	A,W	A	O,U	A,C	R,T	M	A→D	S-1.5	A	A	A→M
S. (Aphantorhaphopsis)	A	A→S	A*,D	V^{1},O,U*	A*→C	R,T	M	S→D	0.5-1.5	A*,F^{1}	A	A→M,L^{1}
S. (Baeomyia)	A	A	A	U	A	R	S,M	D	S-1.5	A	A	T
S. (Ceranthia)	A	S	A*,L	U	A→C*	R	S,M	L,D	S-1.5	A	A	A^{1},L
S. (Pseudosiphona)	A	A*,W	A	V^{1},U	A*→C	R,T,A	M	A→L	S	J,W*	T	T,F*
S. (Siphona)	A*→S	A→S*	A*,L	O,U*	A,C^{3}	R	S,M*	A,D	S-2.0	A	A	A
S. (Siphonopsis)	A	A,W	A	U	C	R,T,A	M	L→D	S-2.0	A*	A	A→M
S. (Uruactia)	A	A^{1},S^{1}	A	U	A	I	M	A	S	A	A	A
Siphona s.l., sp. grp. 1	A	A→S	A	U	A*,C	R,E,T,I,A^{1}	S^{1},M	L→D*	N-3.0^{1}	A	A,T*	A*→M
Siphona s.l., sp. grp. 2	A	A→S	A*,D	U	A*,C	R,E,T,I,A	M	S→D	0.5-S	A	A,T,L	A→M
Siphona s.l., sp. grp. 3	A	A	A	U	A	R,E,T,A^{1}	S^{1},M	L→D*	0.5-1.5	A	L	A/T^{1},T,M
Siphona s.l., unplaced	A	A*→S	A,D^{1}	V^{2},O,U*	A*,C	R,E,T,I,A^{1}	S,M*	S→D	0.5-1.5	A	A*,T	A→M

Table 1 (cont.). Distribution of character states in the Siphonini.

Character	47	48	49	50	51	52	53	54	55	56
	Epiphallus	Male distiphallus			Postgonite	Male surstylus		Cerci	Female	Female
Taxon	size	posterior	posterolateral	lateral	shape	basally	shape	shape	ovipositor	sternum 6
Goniocera	N	I	S	A	W	F	L	I	M	A
Proceromyia	A^{1},S^{1}	I	A	P	W	M	A	A^{1},S^{1}	S^{1}	A^{1}
Entomophaga	S^{1},N^{1}	I	A	P	W	M	A^{1},C^{1}	S	S^{1}	A^{1}
Ceromya s.s.	A,N,P	E^{2},I	A→E	A*,P	W	M,F*	A,B,S,C,L	A,S,I	S→E	A
Ceromya silacea group	A,N^{1}	I	A→E	A,P^{1}	W	M,F	A,C,L	A,S,I	S^{1}	A^{1}
Actia	A	I	A	A*,P	W	M	A,B,S,L	A,S,R,I	S	A
Peribaea	A,N,P	E	A	A,P^{2}	W	M*,F	A,B,C,L	A,S,L,R*	S*→E,V^{1}	A*→E,W,S
Siphona sensu lato										
S. (Actinocrocuta)	A	I	A	A,P	W,S^{1}	M	A,S	L	M^{1}	W^{1}
S. (Aphaniorhapha)	A	I	A	A,P	W	M	A,S,L	A,R^{2}	S^{1}	A^{1}
S. (Aphantorhaphopsis)	A,N,S^{1},P^{1}	I	A→E	A*,P	W,R^{2}	M,F^{1}	A,B,S,C,L	A*,S,I	S	A
S. (Baeomyia)	A	I	A	A	W,S	M	A,C	A,S,I	S	A
S. (Ceranthia)	A	I	M,E*	A,P	W	M	A	A	S→E	A,W,M^{2}
S. (Pseudosiphona)	A	I	A	A,P*	W	M	A,B,C,L	S→E,B,I*	S*→M	A*,W^{1},S^{1}
S. (Siphona)	A	I	A,M^{1}	A*,P	W	M	A*,L	A	S	A
S. (Siphonopsis)	A	I	A	A	W,S,R^{1}	M	A,L^{1}	A*,S,B	S	A
S. (Uruactia)	A	I	A^{1},M^{1}	P	W	M	L	I	—	—
Siphona s.l., sp. grp. 1	A	I	A	A	W→R*	M	A,B,S,C,L	A,B^{1}	S	A
Siphona s.l., sp. grp. 2	A	E^{1},I	A→E	A	W,S^{1},R^{2}	M	A,C,L	A,R,L	S	A
Siphona s.l., sp. grp. 3	A	I	A	A,P^{1}	W,S^{1},R^{1}	M	A	A	S^{1}	A^{1}
Siphona s.l., unplaced	A	I	A→E	A*,P	W*,R^{2}	M	A*,S,C,L	A,S^{1},B^{1},E^{1},L^{2}	S	A,S^{1}

Table 1 (cont.). Distribution of character states in the Siphonini.

Character	57	58	59	60	61	62	63	64	65	66	67
	Female	Female sternum 7		Female	Segment 7	Female	Female	1st instar	Dorsal	Posteroventral margin	
Taxon	tergum 6	apodeme	shape	tergum 7	spiracle	sternum 8	tergum 10	labrum	cornu	abd. seg. 7	abd. seg. 8
Goniocera	L	A	A^1,W^1	L	I	R	P	B^1	P^1	B^1	R^1
Proceromyia	N^1	W^1	A^1	L^1	A^1	A^1	M^1	—	—	—	—
Entomophaga	N^1	W^1	W^1	L^1	A^1	L^1	A/R^1	I^1	P^1	B^1	R^1
Ceromya s.s.	S,L,N	A*→W	A*,W,S^1	A→L	P,I*,A	A	A,M,P	I^1,B	P	B,10^1	R*,S
Ceromya silacea group	L^1	W^1	A^1	L^1	P^1	A^1	P^1	N^1	P^1	B^1	R^1
Actia	A,S,L,N	A,S^1	A	A,S	I	A	M	B	A,?P^1	B	R*,S
Peribaea	L,D	A	A*→L,W,S	S,L*,F	P	L→A*,B	A,R,M	N,I^1	P	B	R
Siphona sensu lato											
S. (Actinocrocuta)	A^1	W^1	W^1	A^1	?	W^1	P^1	B^1	P^1	4^1	S^1
S. (Aphantorhapha)	A/M^1	W^1	A^1	A/S^1	I^1	A^1	P^1	B^1	P^1	4^1	S^1
S. (Aphantorhaphopsis)	A,?	W	A	A,S^1	I	A*,W	A^1,R,M,P	B	P	B^1,2^2,4-8	S
S. (Baeomyia)	A	W	A	A	I	A	A	B	P	6-8	S
S. (Ceranthia)	A	W	W,S,L	A	P	A	P	B	P	6-8	S
S. (Pseudosiphona)	A	W,S^1	A→L,W,S	A,S^1,L^1	I,A^1	A,B^1,S^1	M,P	N*,I	P	2^1,4^2,4-8	R,S^1
S. (Siphona)	A	W	A	A	P	A	A,R	B	P	4	S
S. (Siphonopsis)	A,S,M	W*,S	A,L^1	A,S^1	I	A	M*,P	B	P	4	S
S. (Uruactia)	—	—	—	—	—	—	—	—	—	—	—
Siphona s.l., sp. grp. 1	A	W	A	A	I	A,W^1	R,M,P	B	P	2^2,5^1	S
Siphona s.l., sp. grp. 2	D	W	A	L	P	W	M,P	B^1	P^1	4^1	S^1
Siphona s.l., sp. grp. 3	D^1	W^1	A^1	A^1	I^1	A^1	P^1	B^1	P^1	4^1	S^1
Siphona s.l., unplaced	A,S,D^1	W,S^1	A,S^1	A→L,F^1	I,P^3	A,W^1,S^1	R,M,P	B	P	4^3,6^2,10^1	S

4. CLASSIFICATION OF THE SIPHONINI

4.1 List of major references to the Siphonini

Thryptoceratae Robineau-Desvoidy 1830: 82-102 (unavailable name).
Siphonae Rondani 1845: 31 (original description).
Siphonina Rondani 1856: 59 (*Siphona*; other siphonine genera in Tachinina).
Siphoninae Rondani 1859: 9-11 (Italian species of *Siphona*; other siphonines in Tachininae).
— [Muscidae], Shiner 1862: 517-522 (early classification; species of Austria).
Céromydes and Thryptocérides, Robineau-Desvoidy 1863: 665-728 (early classification).
Thryptoceratidae, Brauer and Bergenstamm 1889: 101-106 (early classification).
Section *Thryptocera*, Brauer and Bergenstamm 1893: 148-152 (early classification).
—, Bezzi and Stein 1907: 381-392 (early Palearctic catalogue).
Section *Thryptocera*, Villeneuve 1924: 34 (Palearctic reclassification).
Group *Thryptocera*, Stein 1924: 123-148 (reclassification and revision of mid-European species).
— [Eutachininae, Group 3], Lundbeck 1927: 448-476 (species of Denmark).
— [Tachininae], Wainwright 1928: 203-209 (species of Britain).
Actiini, Malloch 1930a: 303-310 (species of Australia, all as *Actia*).
Actiini, Malloch 1930b: 120-148 (species of Malaysia, all as *Actia*).
Actiini and Siphonini, Townsend 1936: 129-152 (tribal descriptions and generic keys; very broad tribal limits).
Crocutini, Mesnil 1939: 35-36 (reclassification).
Actiini and Siphonini, Townsend 1940: 187-299 (generic descriptions following 1936 classification).
Siphonini, Emden [van Emden] 1954: 62-68 (species of Britain).
Siphoninae, Mesnil 1954, 41 pp. (reclassification and species of "Congo Belge").
Siphona group, Herting 1957: 454, 458 (female genitalia).
Siphonini, Herting 1960: 58-63 (biology of Palearctic species).
Siphonina, Mesnil 1962-1965: 795-879 (reclassification and revision of Palearctic species).
Siphonina, Sabrosky and Arnaud 1965: 1061-1064 (list of New World species north of Mexico).
Siphonini, Mesnil and Pschorn-Walcher 1968: 163-164 (list of species of Japan).
Siphonini, Guimarães 1971: 164-171 (list of New World species south of United States; broad tribal concept).
Siphonini, Crosskey 1973: 80-81, 136-138, 176 (species of Australia).
Siphonini, Mesnil 1975: 1399-1400 (changes to 1962-1965 Palearctic revision).
Siphonini, Crosskey 1976a: 112-113, 211-214, 291 (species of Oriental region).
Siphonini, Crosskey 1976b: 99-100 (list of British species).
Siphonini, Crosskey 1980: 852-855 (list of Afrotropical species).
Siphonini, Dear and Crosskey 1982: 134-139 (species of the Philippines).
Siphonini, Andersen 1983: 1-15 (revision of Old World genera).
Siphonini, Crosskey 1984: 261-262 (key to Afrotropical genera).
Siphonini, Herting 1984: 120-126 (list of Palearctic species).
Siphonini, Tschorsnig 1985: 88-89 (male genitalia).
Siphonini, Rognes 1986: 72-73 (list of Norwegian species).

4.2 Diagnosis of Siphonini Rondani

The most convincing synapotypy, and hence best diagnostic feature, of the Siphonini is the presence of only two (rather than three) spermathecae in the female reproductive system. This state seems to be universal among siphonines, and is known to be shared with only one other (unrelated) tachinid genus, *Phaenopsis* Townsend (Andersen 1983).

The following combination of character states separates adults of this tribe from other tachinids: Generally 3.0-5.0mm in length, but varied from 2.0-6.5mm. Head (Figs. 1-20) with little sexual dimorphism. Two proclinate orbital setae in both sexes. Eye bare or almost so and three to five frontal setae except in *Proceromyia pubioculata* (eye densely haired and 8-12 frontals; Fig. 3). Aristomere 2 longer than wide, elongate in most species. Proboscis varied from short to long, labella padlike to more than 2X head height.

Thoracic dorsum illustrated in O'Hara (1983a, fig. 2). Prosternum with one to several pair of setulae in most species, bare in few (intraspecifically varied in few species). Katepisternum with three setae arranged in triangle (Figs. 31-32), lower seta varied from hairlike to slightly longer than upper anterior seta. Row of katepisternal hairs anterior to mid coxa present (Fig. 33) or absent (Fig. 34). Three or four postsutural dorsocentral setae. Scutellum with strong basal, lateral and subapical setae, subapicals longest and convergent to crossed, apicals short in most species. One *ad* seta on mid tibia (Fig. 37) in most species, seta absent from few species (Fig. 38) and row of setae present in *Goniocera* species. Wing relatively short and broad (Figs. 21-22), vein R_1 partially incised at midpoint, vein R_{4+5} setulose dorsally from bifurcation of R_{2+3} and R_{4+5} to crossvein *r-m* or beyond, vein *m* smoothly curved in apical sector and ending in wing margin near wing tip (ending close to end of R_{4+5}), anal vein extended to or not extended to wing margin.

Abdomen (O'Hara 1983a, figs. 7-8) ovoid to elongate, with T_{1+2} excavate on basal half. Median discal setae absent from T_{1+2} to T_4. T_{1+2} with 0-1 pair of lateral marginal setae in most species, additional pair present in few species, pair of median marginal setae present in few species of *Goniocera* and *Siphona (Siphona)*. T_3 to T_4 with strong pair each of lateral and median marginal setae, additional marginals present in few species. T_5 with row of marginal setae and in few species with row of weak discal setae.

Male genitalia (O'Hara 1983a, fig. 9) with tergum 6 unsclerotized to moderately broad and sclerotized. Terga 7+8 clearly developed. Epandrium saddle-shaped. Pregonite (Figs. 39-42, 71-106) clearly developed, with membrane anteriorly between apex and basal articulation with hypandrium (possibly synapotypic of the Siphonini, as suggested by Tschorsnig 1985 and discussed in Evolution chapter). Ejaculatory apodeme clearly developed. Aedeagus with or without an epiphallus. Distiphallus (Figs. 107-136) narrowly connected to basiphallus, in most species approximately cylindrical in shape and well sclerotized laterally. Postgonite clearly developed to markedly reduced. Surstylus (Figs. 137-141) linear, relatively unmodified, and basally free or connected with epandrium by a narrow strap-like connection. Cerci (Figs. 142-144) medially incised basally, fused apically.

Female reproductive system with two spermathecae (synapotypic of the Siphonini). Female genitalia (Figs. 43-46, 145-156) unmodified to long and extensible (telescopic), without piercing ability. Tergum 6 absent to dorsally continuous. Tergum 7 absent to present as two moderate-sized lateral sclerites. Spiracle of segment 6 associated with ventrolateral margin of tergum 6, spiracle of segment 7 varied in position from segment 7 to segment 6. Tergum 8 represented by two lateral sclerites, sternum 8 relatively narrow in most species, absent from few. Segment 9 without external sclerites (O'Hara 1983c: 380). Tergum 10 unsclerotized or represented by small median sclerite or two small sclerites. Sternum 10 and paired cerci unmodified.

4.3 Review of major keys to genera and subgenera of the Siphonini

Keys to genera and subgenera of the Siphonini are available for each of the zoogeographic regions of the world except the Neotropics. Each key reflects a classification different from the one adopted here, so each key also differs from the world key presented below. To avoid confusion between those keys and this one, the major differences are summarized here. Specific information about differences in the placement of species can be obtained by comparison of the species lists accompanying most of the works cited below and the descriptions and species lists contained herein in the Classification chapter. Recent keys to species are cited in the Geographic Distribution section of each supraspecific taxon.

The keys considered here are those published in major works since Mesnil's revision of the Palearctic Siphonini in "Die Fliegen der palaearktischen Region" (1962-1965). The most comprehensive in coverage is Andersen's (1983) revision of the Old World Siphonini. This work is broad in scope and contains important new findings about the Siphonini. Andersen's key (pp. 13-14) is easy to use and his classification is similar to the one presented herein. His key differs from the one below in the following respects: the two species of *Entomophaga* are split between *Actia* and *Ceromya*, *Proceromyia macronychia* is included in *Ceromya*, *Proceromyia pubioculata* (type species of *Nipponoceromyia*) was not examined and hence excluded, *Actia* species with atypical features key to *Ceromya* or *Asiphona*, taxa here considered subgenera of *Siphona s.l.* are considered genera, *Siphona (Aphantorhaphopsis)* is called *Asiphona*, few species of *S. (Aphantorhaphopsis)* key to *Ceranthia*, and *S. (Aphantorhaphopsis)* and *S. (Siphona)* [his *Asiphona* and *Siphona*] not adequately distinguished. Most of these differences stem from the relatively few species examined by Andersen during his study. Most of the species which key differently have limited known ranges (mostly non-Palearctic) and/or are rarely collected, so despite the differences in our keys probably 90% of Old World siphonine species will key to the same taxon. Because the key below attempts to provide for accurate generic placement of all species examined (see Materials and Methods), it is necessarily longer and more complex than Andersen's.

Other keys to Old World siphonine genera and subgenera are regional in coverage. The most comprehensive is Mesnil's Palearctic revision cited above (1962-1965), in which all the then known species of Palearctic Siphonini are keyed and described. Mesnil's revision restructured the concept of the Siphonini into its modern form and still provides the only means for identification of most species of Palearctic Siphonini. With respect to the Palearctic fauna, Mesnil's keys to the Siphonini (1962: 797) and subgenera of *Ceromya* (1963a: 829) differ from mine as follows: *Peribaea* called *Strobliomyia*, *Siphona (Aphantorhaphopsis)* called *Siphona (Asiphona)*, *Ceranthia* accorded generic rank, *Proceromyia* as subgenus of *Ceromya*, *Entomophaga exoleta* in *Actia*, *Ceromya monstrosicornis* as type species of *Ceromya (Stenoparia)* and *Entomophaga nigrohalterata* as *C. (Stenoparia) nigrohalterata*. *Nipponoceromyia* (here synonymized with *Proceromyia*) was described after Mesnil's revision. Atypical species of *Actia* and *S. (Aphantorhaphopsis)* are non-Palearctic in distribution.

The remaining Old World regions have received recent treatment by Crosskey. These include a conspectus of Australian Tachinidae (1973), conspectus of Oriental Tachinidae (1976), review of the Tachinidae of the Philippines (Dear and Crosskey 1982), catalogue of

Afrotropical Tachinidae (1980, including Madagascar) and key to genera of Afrotropical Tachinidae (1984, excluding Madagascar). Excluded from these works is a treatment of Australian Tachinidae outside Australia. These works follow the same classification of the Siphonini, so their keys are here compared as one with the key below: atypical *Actia* species key to *Ceromya*, *Siphona s.s.* not then recorded from Australia, *S. (Aphantorhaphopsis)* generally not recognized so most of its species are placed in *Ceromya* and few (with elongate labella) in *Siphona s.s.*, and ranking of subgenera of *Siphona s.l.* as genera. These differences in classification are mitigated by Crosskey's comprehensive species lists for each region, without which the initial stages of almost any revision of a non-Palearctic tachinid group would be an arduous task.

Wood's (1987) recent key to tachinid genera of the Nearctic region provides a valuable and much needed guide to the identification of Nearctic Tachinidae. Wood separates tachinid genera in the first couplet of his key according to presence or absence of setulae on the prosternum. *Goniocera io* (the only New World species of the genus) is varied for this character, though keys as having a bare prosternum. Other siphonines key as having a setulose prosternum, though few of these species are also intraspecifically varied for this character (especially species of *Siphona (Baeomyia)*). Wood's *Siphona* and *Baeomyia* are equivalent to my *Siphona (Siphona)* and *S. (Baeomyia)*, and his *Ceranthia* includes all Nearctic *Siphona s.l.* species exclusive of the last two subgenera.

4.4 Key to adults of the supraspecific taxa and selected species of world Siphonini

1. Lower proepimeral seta strong and directed downward (Fig. 27) (Old World)....... ....*Peribaea* R.-D.

1'. Lower proepimeral seta absent or hair-like (Fig. 28)..2

2.(1') Anal vein not extended to wing margin (Fig. 21); lower katepisternal seta shorter than upper anterior one (Fig. 31)..3

2'. Anal vein extended to wing margin at least as fold (Fig. 22); lower katepisternal seta subequal to or longer than upper anterior one in most species (Fig. 32). 12

3.(2') Mid tibia with row of three or more *ad* setae and setulae (four species; Europe and northeastern North America). .... *Goniocera* B. & B.

3'. Mid tibia with one *ad* seta in most species (Fig. 37), seta reduced or absent in very few (Fig. 38). 4

4.(3') Aristomere 1 distinctly longer than wide (Figs. 4-5) and fore tibia with preapical *ad* seta as long or longer than *d* seta (two European species).............................
.... *Entomophaga* Lioy....5

4'. Most species with aristomere 1 distinctly shorter than wide and fore tibia with preapical *ad* seta shorter than *d* seta, few species with one (but not both) of above states.. 6

5.(4) Three postsutural dorsocentral setae; katepisternum with row of hairs directly anterior to mid coxa, extended upward almost to lower katepisternal seta (as in *Actia* spp., Fig. 33); male genitalia as in Figs. 50, 75 and 110 (Europe; very rarely collected). .... *Entomophaga exoleta* (Meigen)

5'. Four postsutural dorsocentral setae; katepisternum almost bare directly anterior to mid coxa, except for several hairs in posteroventral corner (Fig. 34); male genitalia as in Figs. 51, 76 and 111 (Europe; commonly collected).....................................
.... *Entomophaga nigrohalterata* (Vill.)

6.(4') Katepisternum with row of hairs directly anterior to mid coxa, extended upward almost to lower katepisternal seta (Fig. 33) (cosmopolitan). ....
.... most species of *Actia* R.-D.

6'. Katepisternum almost bare directly anterior to mid coxa, except for several hairs in posteroventral corner (Fig. 34). 7

7.(6') Male sternum 5 with posterior margin approximately V-shaped (Figs. 58-59); pregonite with outer, sclerotized portion short spinose on apical half or less (Figs. 41-42, 85-86); upper part of anepisternum with two setulae (Fig. 31) (presently known only from Malaysia and eastern Australia). ....

....several species of *Actia* R.-D.

7'. Male sternum 5 with posterior margin U-shaped, obtusely angled or almost transverse (Figs. 48-49, 52-57); pregonite bare or with tiny to distinct, uniformly-sized spinules (Figs. 39-40, 73-74, 77-84) (spinules, if present, restricted to membranous portion of pregonite except in several species with extensively sclerotized, ring-shaped pregonite, Fig. 78); upper part of anepisternum with one setula in most species (Fig. 32).. 8

8.(7') Dorsal surface of wing vein R_{4+5} setulose from base to beyond crossvein *r-m* (as in Fig. 21) (cosmopolitan)..

....most species of *Ceromya* R.-D. *sensu lato*....9

8'. Dorsal surface of wing vein R_{4+5} setulose between base and crossvein *r-m* (as in Fig. 22) (Old World)..10

9.(8) Distiphallus bearing unique, infolded and sclerotized structure formed from posterior surface (Fig. 112); pregonite bare (Fig. 84) (Old World).......................

....*Ceromya silacea* (Mg.) species group

9'. Distiphallus without infolded and sclerotized structure (Figs. 113-116); pregonite bare in few species (Fig. 77), with tiny to distinct spinules in most species (Figs. 78-83) (spinules, if present, restricted to membranous portion of pregonite except in several species with extensively sclerotized, ring-shaped pregonite - Fig. 78); (cosmopolitan)..*Ceromya* R.-D. *sensu stricto*

10.(8') Fore tibia with preapical *ad* seta as long or longer than *d* seta; male genitalia with distinctive sternum 5 (Figs. 48-49), pregonite (Figs. 73-74) and distiphallus (Figs. 108-109)..*Proceromyia* Mesnil....11

10'. Fore tibia with preapical *ad* seta shorter than *d* seta; male genitalia not as above in *C. cephalotes* and *C. natalensis*, not examined in *C. monstrosicornis* (these species discussed in Phylogenetics section of *Ceromya s.s.*)..

....three known species of *Ceromya* R.-D. *sensu stricto*

11.(10) Eye densely haired; 8-12 frontal setae (Fig. 3, eye hairs not shown) (Japan). ....*Proceromyia pubioculata* Mesnil & Shima

11'. Eye almost bare; five frontal setae (Fig. 2) (Japan and Kuril Islands)................. ....*Proceromyia macronychia* Mesnil

12.(2') Katepisternum with row of hairs directly anterior to mid coxa, extended upward halfway to lower katepisternal seta (type specimen of *A. completa* from Malaysia) or almost to lower katepisternal seta (as in Fig. 33; *A. fulvicauda* from Malaysia and *A. chrysocera* from the Seychelles Islands)... ....three known species of *Actia* R.-D.

12'. Katepisternum almost bare anterior to mid coxa, except for several hairs in posteroventral corner (Fig. 34)......................................*Siphona* Meigen....13

13.(12') Mid tibia lacking *ad* seta (Fig. 38); aristomere 1 at least 2X longer than wide, subequal in length to aristomere 2 (Fig. 15); 2-3mm long (five species; western North America). .... *S. (Baeomyia* O'Hara)

13'. Mid tibia with one or two *ad* seta on lower half (Fig. 37); aristomere 1 shorter than aristomere 2, in most species shorter than wide (Figs. 13-14, 16-20); average-sized specimens of all but very few species longer than 3mm................14

14.(13') Maxillary palpus cylindrical to tip, markedly reduced to average length (Fig. 16). 15

14'. Maxillary palpus clavate apically, short to long (Figs. 1-15, 17-20)..................16

15.(14) Distiphallus laterally incised and posterolateral arm clearly developed (Fig. 127); pregonite bare in Mauritius sp. 1, with long seta posteriorly in other species (Fig. 94) (Afrotropical, Nearctic, Palearctic and Oriental regions)........................... ....*S. (Ceranthia* R.-D.)

15'. Distiphallus not laterally incised and without posterolateral arm; pregonite bare (two Australian species, Australia sp. 1 and New Guinea sp. 1)........................ ....two undescribed species of *S. (Aphantorhaphopsis* Tnsd.)

16.(14') Proboscis with prementum and labella elongate, labella slightly longer than prementum and in most species longer than eye height (Figs. 25-26); pregonite of male genitalia without seta posteriorly and lacking spinules apically (Fig. 96); female genitalia unmodified (Figs. 43, 45) except in *S. melanura* (over 80 described species; cosmopolitan). .... *S. (Siphona* Mg.)

16'. Proboscis with prementum and labella varied in length, labella in most species padlike to slightly lengthened (Figs. 13-15, 17-19, 23-24), in very few species as long as prementum (Fig. 20); male genitalia varied, in almost all species in which labella are as long as prementum the pregonite has a seta posteriorly and/or tiny spinules apically (Figs. 89-95, 97-98, 100, 102-106); female genitalia varied. 17

17.(16') Old World in distribution (a polyphyletic group of 21 described and many new species) .... *S. (Aphantorhaphopsis* Townsend)

17'. New World in distribution. 18

18.(17') Distiphallus in profile with parallel anterior and posterior margins, with or without spines apically (Figs. 122-123); pregonite long and slender with tiny spinules apically (Fig. 89); cerci broadened in posterior view (Fig. 142); head as in Fig. 13, with labella varied from padlike to moderately lengthened; body mostly yellow with sparse abdominal pruinosity; wing vein R_{4+5} setulose from base to beyond crossvein *r-m* (*S. singularis* complex and one new species; Neotropical). ....
.... *S. (Actinocrocuta* Townsend)

18'. Male genitalia varied, with not more than one of above states; externally varied, but very few species with above states. 19

19.(18') Distiphallus in profile narrow on apical half and with or without enlarged spines apically or anteriorly (Fig. 130); pregonite without spinules anterolaterally (Figs. 97-98); male sternum 5 with apex of apical lobe curved inward (similar to Figs. 62-63); proboscis with labella elongate, 0.7-0.9 prementum length (Figs. 18, 24); wing vein R_{4+5} not setulose beyond crossvein *r-m* (three described and at least 13 new species; western United States and Neotropics). .... S. (*Siphonopsis* Townsend)

19'. Distiphallus in profile broader on apical half than in Fig. 130 and with or without enlarged spines apically and/or anteriorly; pregonite with or without tiny spinules anterolaterally; male sternum 5 with or without apex of apical lobe curved inward; externally varied, but few species with above states. 20

20.(19') Pregonite (Fig. 95) with tiny spinules anterolaterally, broad with two or more tiny setae posteriorly in most species, few species with J-shaped pregonite or only one tiny seta posteriorly; distiphallus triangular in profile in most species (Fig. 128); cerci sharply inflexed at midlength in most species (Fig. 140); head habitus varied, but most species with row of short parafacial hairs extended to lower half of eye, arista haired and proboscis with labella slightly more than half prementum length (Fig. 17) (one described and at least 18 new species; United States to northern Argentina). .... S. (*Pseudosiphona* Townsend)

20'. Pregonite more slender than in Fig. 95, with not more than one seta posteriorly and with or without spinules anterolaterally; distiphallus varied, but not triangular as in Fig. 128; cerci smoothly curved to sharply inflexed; externally varied, but very few species with above states...21

21.(20') Male genitalia with median lobe of sternum 5 flattened (Fig. 68), pregonite bare (no spinules or posterior seta; Fig. 99), distiphallus smoothly tapered in profile (Fig. 131), and cerci sharply inflexed at midlength; body relatively large, 4.0-5.0mm in length; also see Recognition section (one described and one new species; Ecuador and Peru). .... S. (*Uruactia* Townsend)

21'. Male genitalia varied, but with not more than two of the four states above........22

22.(21') Male genitalia with pregonite lacking spinules anterolaterally (Fig. 90; posterior seta present or absent), distiphallus tapered in profile (Fig. 124), and cerci not sharply inflexed at midlength and of average shape (similar to Fig. 144) to slightly broadened (Fig. 143) in posterior view; body relatively small, 2.0-3.5mm in length and dark-colored; also see Recognition section (two described and at least four new species; SW United States to SE Brazil)..*S. (Aphantorhapha* Townsend)

22'. Male genitalia without above combination of states; externally varied (two described and over 40 new species; New World, mostly Neotropical). .... New World *Siphona s.l.* species unplaced to subgenus [See descriptive sections on three species groups and unplaced species of New World *Siphona s.l.*]

4.5 Notes about classification chapter

4.5.1 Notes about lists of included species

Each description of a supraspecific taxon of the Siphonini is followed by a list of included species. Names of species treated as valid are preceded by a letter indicating the region of occurrence of the species, and all named species are followed by full bibliographic and type information (sex, type locality and depository, and whether type examined). The following letters are used to denote region(s) of occurrence of each species:

A	Afrotropical, *sensu* Crosskey and White (1977).
N	Nearctic, *sensu* Griffiths (1980).
O	Oriental, *sensu* Crosskey (1976a).
P	Palearctic, as delimited by the Afrotropical and Oriental regions.
S	Neotropical, *sensu* Griffiths (1980).
U	Australian.

Lists of included species were originally compiled from regional catalogues by Sabrosky and Arnaud (1965), Guimarães (1971), Crosskey (1973, 1976a, 1980) and Herting (1984). This information was then checked and where necessary augmented, many of the types personally examined, and the species and genera reclassified into the present scheme.

Changes to previous classifications are listed in the next section and are indicated in the lists in bold face. In general, I avoided decisions about species synonymies and followed current placements. This is particularly true of the older Palearctic names that have been authoritatively re-evaluated in the works of Herting (1969-1984). For each listed synonym I have included a recent reference to its synonymic status rather than attempt to determine the author who first proposed the synonymy. In a few instances I have recognized new synonymies or have changed the status of subspecies. Each change of this sort is discussed in the taxonomic portion of this revision under the appropriate genus. Not discussed are new combinations unless the species involved possesses a combination of character states unusual or atypical of the genus into which it is placed.

4.5.2 Summary of taxonomic changes

In total, the present classification of the Siphonini includes 385 species names (excluding *nomina nuda* and misspellings), of which 294 are presumed to represent taxonomically valid species. Placement of species into genera and subgenera is based in part on examination of 264 primary types, eight paratypes, and identified specimens of most of the remaining species; types not examined include 31 known to be lost (22 of these being Robineau-Desvoidy nominal species) and 13 not located and possibly lost. Reclassification of the Siphonini is also based on examination of specimens of more than 100 undescribed New World siphonines and numerous undescribed Old World siphonines. Seven genera are recognized within the Siphonini, each presumed to be monophyletic: *Goniocera* Brauer and Bergenstamm, *Proceromyia* Mesnil (elevated from subgeneric status within *Ceromya* and including *Nipponoceromyia* Mesnil and Shima, n. syn.), *Entomophaga* Lioy, *Ceromya* Robineau-Desvoidy (including new synonym *Actinactia* Townsend), *Actia* Robineau-Desvoidy, *Peribaea* Robineau-Desvoidy and *Siphona* Meigen. *Ceromya* is informally divided into *Ceromya s.s.* and the *C. silacea* species group. *Siphona* is a monophyletic taxon wherein diversification from a common groundplan has led to great homoplasy among different lineages. To reflect the uncertain phylogenetic affinities among these lineages and the general cohesiveness of the genus relative to other siphonine genera, *Siphona* is reclassified into the following nine subgenera: *Actinocrocuta* Townsend (new status), *Aphantorhapha* Townsend (new status), *Aphantorhaphopsis* Townsend (new status; an unresolved and possibly polyphyletic group of Old World species, including *Asiphona* Mesnil, n. syn.), *Baeomyia* O'Hara (new status), *Ceranthia* Robineau-Desvoidy (new status), *Pseudosiphona* Townsend (new status), *Siphona* Meigen, *Siphonopsis* Townsend (new status) and *Uruactia* Townsend (new status). Two New World species, *Actia panamensis* Curran and *Aphantorhapha pulla* Reinhard are left unplaced in *Siphona s.l.*

New combinations resulting from reclassification of the Siphonini are: *Nipponoceromyia pubioculata* Mesnil and Shima to *Proceromyia*; *Actia amblycera* Aldrich, *Actia cornuta* Aldrich, *Actinactia lutea* Townsend and *Actia normula* Curran moved to *Ceromya*; *Actia stiglinae* Bezzi moved to *Peribaea*; and 20 species formerly in *Asiphona* Mesnil are provisionally placed in *S. (Aphantorhaphopsis)*. *Actia heterochaeta* Bezzi is left unplaced within the Siphonini. Removed from the Siphonini is *Actia aberrans* Malloch (referred to *Eurysthaea* Robineau-Desvoidy by Crosskey, pers. comm.).

In general the status of named species has been maintained as listed in current literature, though the following new synonymies were recognized and are herein proposed: *Actia brevis* Malloch synonymized with *A. darwini* Malloch, *Peribaea subaequalis* (Malloch) with *P. aegyptia* (Villeneuve), *Actinocrocuta chaetosa* Townsend with *S. (Actinocrocuta) singularis* (Wiedemann), and *Siphona janssensi* with *S. (Siphona) cuthbertsoni* Curran. Elevated from subspecific to species status are: *Ceromya similata* Mesnil, *Siphona (Siphona) infuscata* (Mesnil) and *S. (Siphona) nigrohalterata* Mesnil. Lectotypes are designated for *Ceromya cibdela* (Vill.) and *S. (Pseudosiphona) brevirostris* Coquillett.

4.5.3 Type designations of Coquillett and Townsend

In the late 1800's and early 1900's the type concept became increasingly popular among taxonomists, and it was not unusual for workers of that period to adopt the concept at some point in their careers. Coquillett and Townsend were two such workers, and it is the status of the type series of their earlier species that is of concern here.

It is evident that Coquillett, by the time of his 1897 "Revision of the Tachinidae", was not only choosing type specimens for new species but for his previously described species as well. He assigned type numbers to each of his USNM types, though only published numbers for species he described as new in the "Revision" (Sabrosky, pers. comm.). For previously described species Coquillett generally appended his redescription with the statement "From the type specimen". For the purposes of nomenclatural stability, and because Coquillett's intent is clear, I accept his reference to a type specimen in the redescription of a species described from syntypes as a valid lectotype designation. (This was also the interpretation of Sabrosky and Arnaud 1963.) Similarly, I accept Coquillett's citation of a type number in the description of a new species as sufficient for a holotype designation, provided specimens were labelled appropriately. Under the first situation two siphonines are involved, *S. (Siphonopsis) plusiae* and *Ceromya palloris*, and under the second *S. (Ceranthia) flavipes* and *S. (Pseudosiphona) brevirostris*. In the text that follows I accept Coquillett's lectotype designations of *S. plusiae* and *C. palloris* and his holotype designation of *S. flavipes*. I have had to designate a lectotype for *S. brevirostris* because Coquillett's original holotype designation refers to a pin bearing two specimens, neither of which was specifically chosen as the type.

There is only one siphonine described by Townsend, *Actinocrocuta chaetosa*, for which a holotype was not designated in the original description. However, in his 1940 redescription of the genus (which is herein considered a subgenus of *Siphona*), Townsend cites the "Ht male" of *A. chaetosa*, clearly indicating his choice of the only male of the type series as the type. I accept this citation as a lectotype designation.

4.6 Goniocera Brauer and Bergenstamm

Figs. 1, 47, 71-72, 107, 137, 145, 158.

Goniocera Brauer and Bergenstamm, 1891: 354. Type-species, *G. schistacea* Brauer and Bergenstamm, 1891 (monotypy).

Euthryptocera Townsend, 1916: 624. Type-species, *Tachina latifrons* Meigen, 1824 (original designation) = *Tachina versicolor* Fallén, 1820.

Euchaetactia Villeneuve, 1921: 47 (as subgenus of *Actia* Robineau-Desvoidy). Type-species, *Actia* (*Euchaetactia*) *montium* Villeneuve, 1921 (monotypy).

Cartocometes Aldrich, 1929: 9. Type-species, *C. io* Aldrich, 1929 (original designation).

Recent synonymy by Wood (1987: 1258) in key to Nearctic tachinid genera.

Recognition

This genus of four described species belongs to the group of siphonine genera in which the anal vein does not extend to the wing margin (*i.e.* all genera except *Peribaea* and *Siphona s.l.*), and is distinguished from other members of this group by the presence of several *ad* setae on the mid tibia. Other siphonines have one *ad* seta (Fig. 37) or none (Fig. 38), with the known exception of two undescribed African species of *S. (Aphantorhaphopsis)* which have two setae - these two species have the anal vein extended to the wing margin and other *Siphona s.l.* characteristics. The distinctive shape of the distiphallus is probably autapotypic of *Goniocera* (Fig. 107; refer to Description and Phylogenetics sections).

Three of the four *Goniocera* species have a densely setulose parafacial (Fig. 1). The other species, *G. versicolor*, has the lower parafacial bare as in most other siphonines (several siphonines have hairs on lower parafacial, but fewer hairs than in the three *Goniocera* species). Other features shared by species of *Goniocera*, though only collectively unique to the genus, include (*cf.* Table 1): wing vein R_{4+5} setulose from base to beyond crossvein *r-m* and other veins bare, prominent and flattened median lobe on male sternum 5 (Fig. 47; similar appearance in few *Ceromya* species), surstylus long and basally fused with epandrium (Fig. 137), and reduced female sternum 8 (Fig. 145). The male and female genitalia of *G. montium* and the female genitalia of *G. versicolor* were not examined, so it is unknown if these species share the genitalic features of the other species.

Description

Length: 4.0-6.0mm.

Head (Fig. 1).— Five frontal setae, normal arrangment. Proclinate orbital setae subequal in size in most species. Lower parafacial bare in *G. versicolor*, densely setulose in other species. Eye of male small to medium, 0.58-0.71 head height; eye of female slightly smaller than in male. Flagellomere 1 of male medium-short to medium-long, 0.42-0.67 head height; shape from linear to slightly broadened; not bifid. Flagellomere 1 of female slightly smaller than in male. Aristomere 1 short. Aristomere two 2-4X longer than wide. Aristomere 3 almost bare to micropubescent, rather short (*G. montium*) to long and tapered. Clypeus U-shaped. Palpus short to medium, clavate. Proboscis with prementum short, labella padlike.

Thorax.— Prosternum bare or setulose. Lower proepimeral seta weak, not directed downward. Katepisternum bare anterior to mid coxa. Lower katepisternal seta shorter than upper anterior seta. Three postsutural dorsocentral setae, except four in *G. montium*. Upper part of anepisternum lacking, or with single, setula. Fore tibia with preapical *ad* seta varied: short in *G. montium*, half to subequal length of *d* seta in *G. schistacea*, and at least length of *d* seta in *G. io* and *G. versicolor*. Mid tibia with row of *ad* setae, two to seven long and one to three shorter in most taxa. Tarsomeres normal in size, claws small to medium. Wing: CuA_1 with distal portion 0.26-0.47 length of proximal portion (*i.e. dm-cu* near wing margin; mean 0.34); anal vein not extended to wing margin. Wing setulae: R_1 bare dorsally and ventrally; R_{4+5} setulose from base to beyond *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. Setae varied in length intraspecifically: some specimens with median and lateral marginal setae on T_{1+2} and lateral discal setae on T_{1+2}-T_5, others without long setae on T_{1+2} and with normal setation on T_3-T_5.

Male genitalia (Figs. 47, 71-72, 107, 137).— S_5 (Fig. 47) little varied, posterior margin approximately U-shaped; processes with apical lobes clearly differentiated, at least as long as wide; median lobe unusually prominent, in form of broad, truncate plate flattened posteromedially; processes moderately setulose. T_6 in form of single, narrow to broad, dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion subequal to or slightly wider than hypandrial apodeme. Pregonite in profile either narrow and linear (Fig.

72), or broad and truncate with membranous portion spinulose (*G. io*, Fig. 71). Epiphallus present, narrow (not absent as stated in Andersen 1983 and shown in his fig. 22). Distiphallus (Fig. 107) large, in profile more or less truncate apically and evenly tapered basally, posterolateral margin with short pointed sclerite (not extended beyond apex of distiphallus) separated from broad lateral margin by narrow incision (posterolateral margin curved toward midline and thus pointed sclerite not visible in Fig. 107), anterior margin distinctly developed; apex at least as long as broad in ventral view. Postgonite apically narrow or broad, turned outward. Surstylus long, thin and straight; fused basally with epandrium (Fig. 137). Cerci elongate, sharply inflexed at midlength; thickly covered with long setae on basal half (Fig. 137).

Examined male genitalia of: *G. io, G. schistacea* and *G. versicolor* (last species shown in Andersen 1983, fig. 22).

Female genitalia (Fig. 145).— Moderately extensible. S_6 with very long hairs. T_6 distinctly developed, enclosing spiracles of segment 6; discontinuous dorsally. S_7 without anterior apodeme; pointed posteriorly, with (*G. schistacea*) or without (*G. io*) posteromedial keel. T_7 present as two lateral sclerites; spiracles of segment 7 in membrane between segments 6 and 7. S_8 small, haired. T_{10} present as two small sclerites.

Examined female genitalia of: *G. io*. Female reproductive system of *G. schistacea* shown in Andersen (1983, fig. 3).

First instar (Fig. 158).— Cephalopharyngeal skeleton: Labrum hatchet-like. Lateral sclerite unmodified. Hypopharyngeal sclerite unmodified. Both dorsal and ventral cornua present.

Posterior abdominal segments of first instar ventrally: Segment 7 bare. Segment 8 bare anteriorly; two rows of small spinules posteriorly. Segment 9 bare posteriorly; anus average-sized.

Examined first instar of: *G. io*. Larva of *G. schistacea* (as *G. enigmatica*) shown in Nielsen (1917, figs. 19-20).

Hosts

Hosts are known for three of the four species, and these are all parasites of *Malacosoma* species (tent caterpillars) (Table 2).

Phylogenetics

The only externally autapotypic feature of *Goniocera* is the row of *ad* setae on the mid tibia, though similarities in the male genitalia, specifically sternum 5 and distiphallus, in three of the four species (male genitalia of *G. montium* not examined) provide additional evidence supporting monophyly of the genus. With respect to male sternum 5, the median lobe is unusually prominent, and flattened on its posteromedial surface (Fig. 47). A trend in several siphonine groups is toward a flattened median lobe (*e.g.* Figs. 54, 68), but only in few *Ceromya s.s.* species is its shape similar to that in *Goniocera* species. Considering this trend, and the presumably derived phylogenetic position of these *Ceromya s.s.* species within that genus, it is probable that the characteristic shape of sternum 5 among *Goniocera* species is a synapotypy, and its similar appearance in *Ceromya s.s.* is the result of convergence.

Shape of the distiphallus is similar among examined *Goniocera* species (Fig. 107). In particular the posterolateral margins are curved toward the midline, and incised to form two short sclerotized projections (one per side) - as these projections are only seen in posterior view they are not visible in Fig. 107. The only other siphonines known to share this feature are two species of the *Ceromya palloris* group, *C. flaviseta* and *C. ontario*, which are not otherwise similar to *Goniocera* species. The male genitalia of *G. montium* were not examined, but it is predicted that they have the same states here suggested as synapotypies of the genus.

The pregonite of *G. io* differs from those of *G. schistacea* and *G. versicolor* by the presence of tiny spinules on the membranous portion (Fig. 71). This feature is in most *Ceromya s.s.* species, and is considered synapotypic of that group. The presence of spinules on the pregonite of *G. io* can be interpreted in several ways, as discussed in the Evolution chapter. These different interpretations of the pregonite in *G. io* lead to different phylogenetic senarios regarding *Goniocera* (Figs. 212-215), but none challenges the well established monophyly of the genus.

Adult females of *G. io* and *G. schistacea* have a small sternum 8 (Fig. 145), which is a derived state among siphonines. The size of this sclerite is unknown in *G. montium* and *G. versicolor*, but if also small, then would represent another synapotypy of the genus.

Tent caterpillars (*Malacosoma* species, Lasiocampidae) are the only known hosts of *Goniocera* species (Table 2). Since *G. montium* is the only *Goniocera* species for which a host is unrecorded, and *Malacosoma* species are not known hosts for any other siphonines, I hypothesize that this parasitic specialization is a synapotypy of *Goniocera* species.

Geographic distribution

This genus includes three sympatric species in the Palearctic region, all western in distribution (Mesnil 1963a, Herting 1984): *G. montium* (a rarely collected species only known from France), *G. schistacea* (Denmark and Middle Europe) and *G. versicolor* (ranging from southern Sweden to England, France, Germany, Austria and Poland). The single Nearctic species, *G. io*, is recorded from eastern Canada and northeastern USA (Sabrosky and Arnaud 1965).

List of described species included in Goniocera

N *io* (Aldrich), 1929: 10 (*Cartocometes*). Holotype female, USA: New York, Riverhead (USNM).

P *montium* (Villeneuve), 1921: 47 (*Actia* (*Euchaetactia*)). Holotype male, France: [Col du] Lautaret (CNC). Holotype examined.

P *schistacea* Brauer and Bergenstamm, 1891: 354. Holotype female, Austria (not located).

syn. *enigmatica* Villeneuve and Nielsen *in* Nielsen, 1917: 32. Holotype female, Denmark: Tisvilde (not located).— Mesnil, 1962: 800.

P *versicolor* (Fallén), 1820: 19 (*Tachina*). Syntypes, Sweden: Skåne (NRS).

syn. *hartigii* (Ratzeburg), 1844: 172 (*Musca* (*Tachina*)). Type, Germany (lost).— Herting, 1982: 8.

latifrons (Meigen), 1824: 365 (*Tachina*). Holotype female, Austria (lost).—

Herting, 1984: 120.

ludibunda (Robineau-Desvoidy), 1850: 195 (*Ceromya*). Syntypes, France (lost).— Herting, 1974: 18.

4.7 Proceromyia Mesnil

Figs. 2-3, 48-49, 73-74, 108-109, 146.

Proceromyia Mesnil, 1957: 35 (as subgenus of *Ceromya*). Type-species, *Ceromya* (*Proceromyia*) *macronychia* Mesnil, 1957 (monotypy).

Nipponoceromyia Mesnil and Shima, 1978: 324. Type-species, *N. pubioculata* Mesnil and Shima, 1978 (original designation). **New synonymy.**

Recognition

The two described species of *Proceromyia* are only recorded from Japan and the Kuril Islands. One, *P. pubioculata*, is markedly autapotypic in external head features, differing from other siphonines in having a densely haired eye and 8-12 frontal setae (Fig. 3). The other species, *P. macronychia*, is less distinctive and easily mistaken externally for a *Ceromya* species (head shown in Fig. 2). Both species share externally the following unique combination of character states (*cf.* Table 1): narrow vertex (apparently unique, but not quantitatively assessed in this study), prosternum bare (rare among siphonines), fore tibia with preapical *ad* seta subequal in length or longer than *d* seta (as in *Entomophaga* species and several other species), large tarsal claws (only as large in some *Siphona s.s.* species), wing vein R_{4+5} setulose between base and crossvein *r-m* and other veins bare, and anal vein not extended to wing margin.

Features of the male genitalia, particularly shape of sternum 5 (Figs. 48-49), pregonite (Figs. 73-74) and distiphallus (Figs. 108-109) are also diagnostic for the genus, though the latter two structures closely resemble those in the sister genus *Entomophaga* (Figs. 75-76 and 110-111). *Proceromyia* species are distinguished externally from those of *Entomophaga* by their short aristomere 1 (*cf.* Figs. 2-3 and 4-5), bare prosternum and larger tarsal claws.

Description

(Note: female of *P. pubioculata* unknown.)

Length: 3.0-5.5mm.

Head (Figs. 2-3).— (Head of *P. pubioculata* also shown in Mesnil and Shima 1978, fig. 10.) Generally five frontal setae in *P. macronychia*, 8-12 in *P. pubioculata*, rather fine in both. Proclinate orbital setae thin but average length, subequal in most specimens. Eye almost bare (*P. macronychia*) or densely haired (*P. pubioculata*). Eye of male and female subequal, medium-large, 0.78-0.84 head height. Flagellomere 1 of male short to medium-short, 0.34-0.43 head height; shape average in width; not bifid. Flagellomere 1 of female usually slightly smaller than in male. Aristomere 1 short. Aristomere two 1.5-3X longer than wide. Aristomere 3 almost bare, slightly short to normal length, evenly tapered to tip or abruptly narrowed on apical two-thirds. Clypeus U-shaped in *P. macronychia*, not examined in *P. pubioculata*. Palpus short to medium, clavate. Proboscis with prementum short, labella padlike.

Thorax.— Prosternum bare. Lower proepimeral seta weak, not directed downward. Katepisternum bare anterior to mid coxa. Lower katepisternal seta shorter than upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with single setula in *P. macronychia*, with three setulae in single examined specimen of *P. pubioculata*. Fore tibia with preapical *ad* seta subequal to or longer than *d* seta. Mid tibia with one *ad* seta. Tarsomeres normal in size; claws large. Wing: CuA_1 with distal portion 0.24-0.32 length of proximal portion (*i.e.* *dm-cu* near wing margin; mean 0.27); anal vein not extended to wing margin. Wing setulae: R_1 bare dorsally and ventrally; R_{4+5} setulose between base and *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae; lateral marginal setae strong. T_3-T_5 average or with lateral discal setae on one or more segments.

Male genitalia (Figs. 48-49, 73-74, 108-109).— S_5 (Figs. 48-49) little varied, posterior margins of processes obtusely angled; apical lobe slightly differentiated; median lobe rounded, relatively unmodified; processes moderately setulose. T_6 forming single, broad, dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion slightly wider to about 1.5X wider than hypandrial apodeme. Pregonite (Figs. 73-74) in profile smoothly curved anteriorly and more or less pointed apically, with small spines along anterolateral ridge. Epiphallus small in *P. pubioculata*, absent from *P. macronychia*. Distiphallus (Figs. 108-109) with posterior margin partially reduced, laterally incised, anterior margin reduced except for long, spined anterolateral arm; apex broader than long in ventral view. Postgonite apically broad and turned outward. Surstylus average length, broadened at midlength, straight; basally free from epandrium. Cerci rather short (*P. macronychia*) to average length (*P. pubioculata*), smoothly curved at midlength; moderately setose on basal half.

Examined male genitalia of: *P. macronychia* and *P. pubioculata* (latter shown in Mesnil and Shima 1978, fig. 11).

Female genitalia (Fig. 146).—(Only *P. macronychia* examined.) Short. S_6 with short hairs. T_6 distinctly developed, enclosing spiracles of segment 6; narrowly discontinuous dorsally. S_7 with long anterior apodeme; without posteromedial keel. T_7 present as two lateral sclerites; spiracles of segment 7 displaced anteriorly and enclosed in posterior margin of T_6. S_8 distinctly developed, haired. T_{10} present as small median sclerite.

Examined female genitalia of: *P. macronychia*.

First instar.— Not examined.

Hosts. Unknown.

Phylogenetics

Mesnil described *P. macronychia* in 1957 (p. 35) as a new species in new subgenus *Ceromya (Proceromyia)*, basing the new taxon primarily on the presence of large claws and narrow vertex. At that time *Ceromya s.l.* was recognized as a siphonine genus in which the anal vein did not extend to the wing margin and from which the derived features of *Actia* and *Goniocera* were lacking.

Mesnil later completely revised the Palearctic *Ceromya* species (1963a: 829), and recognized two primary divisions within the genus: *Ceromya (Ceromya)* characterized by wing vein R_{4+5} setulose from base to beyond crossvein *r-m*, and both *C. (Proceromyia)* and *C. (Stenoparia)* characterized by vein R_{4+5} not setulose beyond *r-m*. I discuss here the monophyly of Mesnil's *C. (Proceromyia)* - status of *C. (Stenoparia)* and placement of its type species *C. montrosicornis* are discussed in the Phylogenetics section of *Ceromya s.s.*, while the other *C. (Stenoparia)* species recognized by Mesnil, *C. nigrohalterata*, is placed in *Entomophaga* and discussed in the Phylogenetics section of that genus.

The second species here included in *Proceromyia* is a siphonine of unusual appearance, *P. pubioculata*. This species was described in its own genus, *Nipponoceromyia* Mesnil and Shima (1978), primarily because of its uniquely haired eye and numerous frontal setae (Fig. 3). The authors commented that *P. pubioculata* seemed related to *Proceromyia macronychia* (1978: 325), citing as evidence the shared possession of weak proclinate orbital setae, narrow vertex and short distal section of wing vein CuA_1. I doubt that the first character state is uniquely shared by these two species, the last certainly is not, but the narrow vertex might be a synapotypy of these species. Both species also have unusually large tarsal claws. The male genitalia of *Proceromyia macronychia* and *Nipponoceromyia pubioculata* were apparently not compared by Mesnil and Shima, but corroborate their phylogenetic hypothesis and as discussed below provide better evidence for a sister species relationship between these species.

Similarities in the male genitalia of *Proceromyia macronychia* and *Nipponoceromyia pubioculata* belie the external differences between these species, leading to the conclusion that the autapotypic features of *N. pubioculata* are the result of divergence from a more *P. macronychia*-like ancestor. In support of this are the remarkable similarities in male sternum 5 (Figs. 48-49), pregonite (Figs. 73-74) and distiphallus (Figs. 108-109) - similarities which also attest to a close relationship with *Entomophaga* (see the Phylogenetics section of that genus and the Evolution chapter for a discussion of these intergeneric relationships). Given the general external similarities between *P. macronychia* and *P. pubioculata* (listed in Recognition section) and diverse shapes of male genitalia among siphonines in general, I regard the shared similarities in male genitalia of these two species as synapotypies. I propose the following classification to reflect this hypothesized relationship between *P. macronychia* and *N. pubioculata*: *N. pubioculata* is moved to *Proceromyia*, and *Proceromyia* is ranked at the generic level because of its sister group relationship with *Entomophaga*, and its lack of known synapotypies with *Ceromya*. Both *Proceromyia* and *Nipponoceromyia* were ranked as monobasic genera by Herting (1984: 121-2) before the male genitalia of the two included species were compared (in contrast, Andersen 1983 placed *Proceromyia* as a synonym of *Ceromya* and did not study *Nipponoceromyia*). It seems appropriate to modify Herting's classification of these two species by combining them under one generic name now that their genitalic features are known to be so similar.

Geographic distribution

The known ranges of the two included species are very limited: *P. macronychia* was described from Hokkaido, Japan, and has since been recorded from the Kuril Islands, USSR (Richter 1976b). *P. pubioculata* is only known from male specimens collected from Honshu Island, Japan.

List of described species included in Proceromyia

P *macronychia* (Mesnil), 1957: 35 (*Ceromya* (*Proceromyia*)). Holotype male, Japan: Hokkaido, Obihiro (CNC). Holotype examined.

P *pubioculata* (Mesnil and Shima), 1978: 325 (*Nipponoceromyia*). Holotype male, Japan: Honshu, Kawaragoya (BLKU). Paratype examined. **New combination.**

4.8 Entomophaga Lioy

Figs. 4-5, 50-51, 75-76, 110-111, 147, 159.

Entomophaga Lioy, 1864: 1332. Type-species, *Tachina exoleta* Meigen, 1824 (by designation of Coquillett, 1910: 538).

Recognition

Entomophaga comprises two described European species, *E. nigrohalterata* and *E. exoleta*. The former is commonly collected while the latter is known from very few specimens. A diagnostic combination for these species is the possession of an elongate aristomere 1 (Figs. 4-5), fore tibia with preapical *ad* seta subequal in length or longer than *d* seta, wing vein R_{4+5} setulose between base and crossvein *r-m* and other veins bare, and anal vein not extended to wing margin (*cf.* Table 1). In addition, features of the male genitalia are distinctive, and are similar only to the male genitalia of the externally very different appearing *Proceromyia* species (*cf.* head profiles in Figs. 2-5, sternum 5 in Figs. 48-51, pregonite in Figs. 73-76 and distiphallus in Figs. 108-111).

Entomophaga exoleta has been considered an *Actia* species by some authors because of its row of hairs on the katepisternum anterior to the mid coxa (as in Fig. 33), but is clearly misplaced there based on other features (see Phylogenetics section and Evolution chapter). Likewise, *E. nigrohalterata* has been mistaken for a *Ceromya* species because its phylogenetically important character states have been misinterpreted.

Description

Length: 3.0-5.0mm.

Head (Figs. 4-5).— Four or five frontal setae, in normal arrangement. Anterior proclinate orbital seta longer than posterior one in *E. exoleta*, setae subequal in length in *E. nigrohalterata*. Eye bare. Eye of male small to medium, 0.63-0.77 head height; eye of female slightly larger than in male. Flagellomere 1 of male medium to medium-long, 0.58-0.66 head height; shape broad to subquadrangular; not bifid. Flagellomere 1 of female slightly smaller than in male. Aristomere 1 elongate, 1.5-5X longer than wide. Aristomere two 3-4X longer than wide. Aristomere 3 almost bare, slightly shorter than average, evenly tapered to tip. Clypeus U-shaped. Palpus long, clavate. Proboscis with prementum short, labella padlike.

Thorax.— Prosternum setulose. Lower proepimeral seta weak, not directed downward. Katepisternum bare (*E. nigrohalterata*) or with row of hairs anterior to mid coxa (*E. exoleta*). Lower katepisternal seta shorter than upper anterior seta. Three (*E. exoleta*) or four (*E. nigrohalterata*) postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta subequal to or longer than *d* seta. Mid tibia with one *ad* seta. Tarsomeres normal in size, claws small to medium-large. Wing: CuA_1 with distal portion 0.25-0.43 length of proximal portion (*i.e. dm-cu* near wing margin; mean 0.33); anal vein not extended to wing margin. Wing setulae: R_1 bare dorsally and ventrally; R_{4+5} setulose between base and *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae; lateral marginal setae strong. T_3-T_5 average or with lateral discal setae on 1 or more segments.

Male genitalia (Figs. 50-51, 75-76, 110-111).— S_5 with apical lobe of processes slightly differentiated (posterior margins almost transverse, Fig. 51) in *E. nigrohalterata*, distinctly differentiated and posterior margin approximately U-shaped in *E. exoleta* (Fig. 50); median lobe rounded, relatively unmodified; processes moderately setulose. T_6 forming single, broad, dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion slightly wider to almost 2.0X wider than hypandrial apodeme. Pregonite in profile smoothly curved anteriorly, pointed apically; either bare (*E. nigrohalterata*, Fig. 76) or spined along anterolateral margin (*E. exoleta*, Fig. 75). Epiphallus present: very short in *E. nigrohalterata*, long and narrow in *E. exoleta*. Distiphallus (Figs. 110-111) with posterior margin partially reduced, laterally incised, anterior margin reduced except for long, spined anterolateral arm; broader than long in ventral view. Postgonite apically broad and turned outward. Surstylus average length, straight (*E. nigrohalterata*) or curved posteriorly (*E. exoleta*); basally free from epandrium. Cerci rather short, smoothly curved at midlength; moderately setose on basal half.

Examined male genitalia of: *E. exoleta* and *E. nigrohalterata* (latter shown in Andersen 1983, fig. 24).

Female genitalia (Fig. 147).— (Only *E. nigrohalterata* examined.) Short. S_6 with very short hairs. T_6 distinctly developed, enclosing spiracles of segment 6; narrowly discontinuous dorsally. S_7 with long anterior apodeme; slightly keeled posteromedially. T_7 present as two lateral sclerites; spiracles of segment 7 displaced anteriorly to very near or associated with T_6. S_8 absent. T_{10} absent or present as two small sclerites.

Examined female genitalia of: *E. nigrohalterata* (Andersen 1983, fig. 9).

First instar (Fig. 159).— Cephalopharyngeal skeleton: Labrum slightly broadened anteriorly; angled slightly downward. Lateral sclerite small. Hypopharyngeal sclerite unmodified. Both dorsal and ventral cornua present.

Posterior abdominal segments of first instar ventrally: Segment 7 bare. Segment 8 with tiny spinules anteriorly; uneven row of small spinules posteriorly. Segment 9 bare posteriorly; anus small.

Examined first instar of: *E. nigrohalterata*.

Hosts. Unknown.

Phylogenetics

Herting (1975: 4) revised the standard classification of *E. exoleta* and *E. nigrohalterata* by removing the former from *Actia* and the latter from *Ceromya*, and uniting them under a newly defined *Entomophaga* Lioy (*cf.* Mesnil 1963a). Herting based his concept of *Entomophaga* primarily on two characteristics shared by *E. exoleta* and *E. nigrohalterata*: an elongate aristomere 1 and long preapical *ad* seta on fore tibia. The second feature is shown in this study to be shared with related taxa (see Evolution chapter), but the first is accepted here as a synapotypy of *Entomophaga*, though not unique to the genus (Table 1).

Recently Andersen (1983: 12) reviewed the Old World Siphonini and re-assigned *E. exoleta* to *Actia* and *E. nigrohalterata* to *Ceromya*. Andersen returned *E. exoleta* to *Actia* because he considered its row of katepisternal hairs to be clear evidence of its membership in *Actia*. He interpreted the elongate aristomere 1 of *E. exoleta* and *E. nigrohalterata* as autapotypies of each species, consequently returning the latter to *Ceromya* because "it does not differ significantly from other *Ceromya* species in external characters" (1983: 12). However, Andersen noted that the male and female genitalia of *E. nigrohalterata* were different from the *Ceromya*-type.

Andersen's classification of the two species here placed in *Entomophaga* and *Proceromyia* was based on external characters, since only the genitalia of *E. nigrohalterata* were examined. I hypothesize that characteristics of the male genitalia of the four *Entomophaga* and *Proceromyia* species indicate that these species form a monophyletic lineage, based on shape of the pregonite (Figs. 73-76) and distiphallus (Figs. 108-111), which are derivable from a common groundplan and lack synapotypies with the *Actia* and *Ceromya* lineages. The two *Proceromyia* species are not only remarkably similar in male genitalic features (Figs. 48-49, 73-74, 108-109) but share unique external similarities as well, so are certainly sister species. The male genitalia of *Entomophaga* species are more equivocal: they clearly indicate a close relationship with *Proceromyia*, but not a sister species relationship between *E. exoleta* and *E. nigrohalterata*. However, given the general external similarities between *E. exoleta* and *E. nigrohalterata*, particularly head habitus (Figs. 4-5) and derived state of aristomere 1, these species most probably form a monophyletic group. If these external similarities are not synapotypies then *Entomophaga* might be paraphyletic with respect to *Proceromyia* (*i.e.* either *E. exoleta* or *E. nigrohalterata* being more closely related to the *Proceromyia* lineage than to its congener).

Features of the male genitalia of *E. exoleta* not only corroborate its placement in the *Entomophaga*+*Proceromyia* lineage, but provide the best evidence for removing this species from *Actia*. *Actia* species share the synapotypies of a more or less V-shaped sternum 5 (Figs. 58-59) and apically spinose pregonite (Figs. 85-86), and these states are lacking from *E. exoleta*. It is concluded that the row of katepisternal hairs that are found (among siphonines) only in *E. exoleta* and most *Actia* species is the result of convergence; convergence certainly accounts for the presence of this row of hairs in *Actia* and some non-siphonine tachinids. *E. exoleta* also has one seta on the upper portion of the anepisternum while almost all *Actia* species have two (*cf.* Figs. 31 and 32).

E. nigrohalterata has not been shown to share any synapotypies with *Ceromya*, neither here nor by previous authors. Spinules on the membranous portion of the pregonite in most *Ceromya s.s.* species, here considered a groundplan condition (and synapotypy) of *Ceromya s.s.*, are absent from *E. nigrohalterata*. Further research is needed to resolve relationships within *Ceromya s.l.*, and will not only provide information relevant to the placement of *E.*

nigrohalterata, but to species of *Entomophaga* and *Proceromyia* as well.

Adult females of *E. nigrohalterata* are atypical in their lack of a sclerotized abdominal sternum 8 (Fig. 147). Study of the female genitalia of *E. exoleta* has not yet been possible, but if sternum 8 is lacking then a sister species relationship between *E. exoleta* and *E. nigrohalterata* would be corroborated (otherwise this loss might be autapotypic of *E. nigrohalterata*). It would similarly be useful to compare the first instars of *E. exoleta* and *E. nigrohalterata*.

Similar in some respects to the species of *Entomophaga* is *Ceromya monstrosicornis*. Its placement is discussed in the Phylogenetics section of *Ceromya s.s.*

Geographic distribution

E. exoleta is a rarely collected species, recorded from few localities in France (type locality, and a female in SMNS), Hungary (Andersen, pers. comm.) and England (Crosskey 1976b). *E. nigrohalterata* is a relatively common species in Europe, with records from England, Belgium, Denmark, Germany, Poland, Austria and Switzerland (Mesnil 1963a, Herting 1967b, 1984, Draber-Mońko 1978, 1981). *E. exoleta* and *E. nigrohalterata* are at least narrowly sympatric, with the former slightly more southern in distribution.

List of described species included in Entomophaga

P *exoleta* (Meigen), 1824: 353 (*Tachina*). Syntypes, France: Provence (MNHN).

syn. *anicula* (Meigen), 1824: 409 (*Tachina*). Holotype female, Europe (MNHN).— Herting, 1975: 2.

P *nigrohalterata* (Villeneuve), 1921: 45 (*Actia*). Holotype male, Denmark (CNC). Holotype examined.

syn. *articulata* (Stein), 1924: 131 (*Actia*). Syntypes, Copenhagen, Denmark and Löbauer Berg, German Democratic Republic (ZMUC; not located, maybe lost).— Lundbeck, 1927: 465.

sufferta (Villeneuve), 1942b: 133 (*Actia*). Holotype male, Germany: no locality given (CNC).— Herting, 1981: 8. Holotype examined.

4.9 Ceromya Robineau-Desvoidy sensu lato

Figs. 6-7, 35, 37, 39-40, 52-57, 77-84, 112-116, 138, 148-150, 157, 160-167.

Note about classification of Ceromya s.l. species

No known features are clearly interpretable as synapotypic of *Ceromya s.l.*, and as a result the monophyly of this diverse and cosmopolitan genus has not been positively established. However, features of the male genitalia suggest that *Ceromya s.l.* comprises two monophyletic lineages. These are here called *Ceromya s.s.* (including type species *C. bicolor*) and the *C. silacea* species group (an informal species group in which *C. silacea* is the most apotypic species and has the oldest name), and are treated individually throughout this paper.

The unusual division of *Ceromya s.l.* into two categories of different rank is adopted for practical and nomenclatural reasons. Firstly, male genitalia were not studied in all *Ceromya s.l.* species, so characterization of the lineages may be incomplete, as well as assignment of described species to the *C. silacea* species group. Secondly, recognition of the *C. silacea* species group as a subgenus would require erection of a new genus-group name, which is premature on the basis of available evidence.

Recognition

Ceromya s.l. belongs to the group of siphonines in which the anal vein is not extended to the wing margin (Fig. 21). This characteristic separates all known *Ceromya s.l.* species from species of *Peribaea* and *Siphona s.l.* Additionally, the lower katepisternal seta is shorter than the upper anterior one in all but very few *Ceromya s.l.* species (Fig. 31) while subequal in length or longer in most *Peribaea* and *Siphona s.l.* species (Fig. 32; see Table 1).

New World species of *Ceromya s.l.* are easily separable from other New World siphonines by the following combination of states: anal vein not extended to wing margin (Fig. 21), absence of row of hairs on katepisternum (Fig. 34; row present in all New World *Actia* species, Fig. 33) and only one *ad* seta on mid tibia (Fig. 37; row of *ad* setae in *Goniocera io*, the only New World *Goniocera* species).

Four Old World genera - *Goniocera, Actia, Entomophaga* and *Proceromyia* - are characterized along with *Ceromya s.l.* by an anal vein not extended to the wing margin. All

Goniocera species have a row of *ad* setae on the mid tibia (0-1 seta in *Ceromya s.l.* species, as in Figs. 37-38) and are separable from *Ceromya s.l.* species by this feature. The diagnosis given above for New World *Ceromya s.l.* species will not separate Old World members of this taxon from species of *Entomophaga* or *Proceromyia*, or several *Actia* species. It is therefore necessary to diagnose Old World *Ceromya s.l.* species by the presence of at least six of the following seven states: 0-1 anepisternal setula, lower katepisternal seta shorter than upper anterior one, katepisternum lacking row of hairs, fore tibia with short preapical *ad* seta, mid tibia with 0-1 *ad* seta, wing vein R_{4+5} setulose beyond crossvein *r-m* and anal vein not extended to wing margin. Similarities and differences among Old World *Ceromya s.l.* species and Old World *Actia*, *Entomophaga* and *Proceromyia* species are discussed below.

Most Old World *Actia* species are distinguishable from *Ceromya s.l.* species by presence of a row of katepisternal hairs (Fig. 33), but very few Old World *Actia* species lack this row of hairs and must be recognized by other features (externally by presence of two anepisternal setulae, though characteristics of the male genitalia provide the best means by which to recognize *Actia* species - see Recognition section of *Actia*).

The four species of *Entomophaga* and *Proceromyia* share two states which in combination distinguish them from *Ceromya s.l.* species: fore tibia with preapical *ad* seta subequal in length or longer than *d* seta (only shared with two *Ceromya* species: Nepal sp. 1 and Australia sp. 3) and wing vein R_{4+5} not setulose beyond crossvein *r-m* (same in three *Ceromya* species: *C. cephalotes*, *C. monstrosicornis* and *C. natalensis*). Features of pregonite and distiphallus are also unique to the *Entomophaga*+*Proceromyia* lineage.

Male genitalic features of *Ceromya s.l.* species are discussed in the Recognition sections of *Ceromya s.s.* and *C. silacea* species group. The possible monophyly of *Ceromya s.l.* is discussed in the Evolution chapter.

4.10 Ceromya Robineau-Desvoidy sensu stricto

Figs. 6-7, 39-40, 53-57, 77-83, 113-116, 138, 149-150, 157, 161-167.

Ceromya Robineau-Desvoidy, 1830: 86. Type-species, *C. testacea* Robineau-Desvoidy, 1830 (by designation of Coquillett, 1910: 520) = *Tachina bicolor* Meigen, 1824.

Ceromyia. Variant spelling of *Ceromya*.

Polychaetoneura Walton, 1914: 90. Type-species, *P. elyii* Walton, 1914 (original designation) = *Thryptocera americana* Townsend, 1892. Recent synonymy by Wood (1987: 1239) in key to Nearctic tachinid genera.

Xanthoactia Townsend, 1919: 585. Type-species, *Lasioneura palloris* Coquillett, 1895 (original designation). Recent synonymy by Wood (1987: 1239) in key to Nearctic tachinid genera.

Stenoparia Stein, 1924: 128. Type-species, *S. monstrosicornis* Stein, 1924 (monotypy).

Schizoceromyia Townsend, 1926b: 542. Type-species, *Schizotachina fergusoni* Bezzi, 1923 (original designation).

Actinactia Townsend, 1927: 248. Type-species, *A. lutea* Townsend, 1927 (original designation). **New synonymy.**

Schizactiana Curran, 1927b: 356 (as subgenus of *Actia*). Type-species, *Actia* (*Schizactiana*) *valida* Curran, 1927 (original designation).

Pseudactia Malloch, 1930b: 124 (as subgenus of *Actia*). Type-species *Actia* (*Pseudactia*) *hirticeps* Malloch, 1930 (monotypy).

Recognition

Features of the male genitalia provide the only means for placing *Ceromya s.l.* species into *Ceromya s.s.* or the *Ceromya silacea* species group. The following characteristics of the male genitalia distinguish species of *Ceromya s.s.* from those of the *C. silacea* species group: pregonite with enlarged membranous area anteriorly, with tiny spinules in most species (Figs. 39-40, 77-83; similar in *Goniocera io* (Fig. 71), otherwise unique to *Ceromya s.s.* species); and distiphallus without infolded, sclerotized structure posteriorly (Figs. 113-116; *cf. C. silacea*, Fig. 112).

External features of specimens of most described *Ceromya s.l.* species were examined during this study, but male genitalia were examined in specimens of only a portion of these species (as listed in descriptions of male genitalia of *Ceromya s.s.* and *C. silacea* sp. grp.). Possibly a complete study of the male genitalia of all species listed in *Ceromya s.s.* will reveal several species that should be reassigned to the *C. silacea* species group. The evidence available at this time is insufficient to permit a thorough reclassification of *Ceromya s.l.* species into *Ceromya s.s.* and *C. silacea* species group.

Description

Length: 3.0-6.0mm.

Head (Figs. 6-7).— Five frontal setae in most species, three or four in very few; normal arrangement. Anterior proclinate orbital seta longer than posterior one in most species. Eye size of male medium-small to large, 0.68-0.86 head height; eye of female slightly smaller to slightly larger than in male, in most species eye size of sexes subequal. Flagellomere 1 of male markedly varied in length, 0.38-0.80 head height; shape from linear to subquadrangular, bifid in *C. fergusoni*, *C. invalida* and *C. valida*, normal in others. Flagellomere 1 of female smaller than in male; not bifid. Aristomere 1 short. Aristomere two 1.5-6X longer than wide in species with normal antenna, up to 10X in species with bifid flagellomere 1. Aristomere 3 short and thickened to near tip, to long and evenly tapered; almost bare, micropubescent, or rarely short plumose. Clypeus U-shaped in most species, narrow and enclosed in membrane in few. Palpus short in most species, medium to long in few; enlarged apically in females of few species; clavate. Proboscis with prementum short, labella padlike (labella very slightly lengthened in *C. luteicornis*).

Thorax— Prosternum setulose in most species, bare in very few. Lower proepimeral seta weak, not directed downward except in very few species (though not long as in *Peribaea* species). Katepisternum bare anterior to mid coxa. Lower katepisternal seta much shorter than upper anterior seta in most species, slightly shorter or subequal to it in two closely related species: *C. flaviseta* and *C. ontario*. Three or four postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta in almost all species, known to be as long as *d* seta only in Nepal sp. 1 and Australia sp. 3. Mid tibia without *ad* seta in *C. fergusoni*, one *ad* seta in other species. Tarsomeres normal in size in most species, with tarsomere 5 of fore leg elongate and broadened in female of several species; tarsomere 5 of all legs elongate and dilated in female of Australia sp. 3; claws short in most species, medium in few. Wing: CuA_1 with distal portion 0.24-0.67X length of proximal portion (mean 0.40); anal vein not extended to wing margin. Wing setulae: R_1 dorsally bare, or distally or entirely setulose, ventrally bare or distally setulose; R_{4+5} setulose from base to beyond *r-m* in most species, not beyond *r-m* in *C. cephalotes*, *C. natalensis* and *C. monstrosicornis*. CuA_1 bare or setulose, with basal section setulose in *C. americana* complex, *C. languidula*, Brazil spp. 1 and 4 (bare in other siphonines).

Abdominal terga 1-5.— Abdomen ovoid in shape in almost all species, slightly elongate in very few. T_{1+2} without median marginal setae; lateral marginal setae absent to strong. T_3-T_5 average in most species, with weak lateral discal setae (T_3-T_5) and/or extra pair of lateral marginal setae (T_3 and T_4 only) in few.

Male genitalia (Figs. 39-40, 53-57, 77-83, 113-116, 138).— S_5 markedly varied, inner (or posterior) margins of processes obtusely angled (Fig. 55) to transverse (Fig. 57), in most species U-shaped (Figs. 53-54, 56); apical lobe usually undifferentiated (Fig. 57) to narrowly pointed, in very few species distinctly differentiated and apically curved inward (Fig. 56); median lobe markedly varied, from rounded (Figs. 55-56) or elongate (Fig. 53) to flattened plate of varied forms (Fig. 54; rarely similar to shape in *Goniocera*), and with or without accessory lobe; processes sparsely to densely setulose. T_6 varied from two very small lateral sclerites to a single, broad, dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion 0.5-1.5X width of hypandrial apodeme. Pregonite in profile extremely varied: membranous anterior portion of pregonite enlarged in most species and usually with spinules anterolaterally (Figs. 39-40, 79-83; these often tiny and visible only at higher magnifications, 100-400X); in one species (*C. lutea*, Fig. 83) pregonite elongate and curved posteriorly (unique within the Siphonini); in one Old World group pregonite ring-shaped and spinules borne anteriorly on sclerotized portion (Fig. 78). Epiphallus present or absent. Distiphallus (Figs. 113-116) extremely varied: in most species anterior margin incised, posterior margin entire in *C. lutea* (Fig. 116) and Nepal sp. 1, at least partially incised in other species, in profile distiphallus laterally incised to varied degrees in most species (Figs. 114-116), lateral margin entire apically in few (Fig. 113). Postgonite large, apically rounded, curved ventrally, or bilobed. Surstylus short to long, thin to broad (Fig. 138), straight or curved posteriorly; with long hairs along length in *C. languidula* (and in *C. varichaeta* of *Ceromya silacea* sp. grp.); basally fused with epandrium in most species (Fig. 138), free in others. Cerci short to average length, deeply inflexed at midlength in some species (Fig. 138), smoothly curved in others; moderately to densely (Fig. 138) setose on basal half.

Examined male genitalia of: *C. amblycera*, *C. americana* complex, *C. cornuta*, *C. flaviceps*, *C. flaviseta*, *C. invalida*, *C. languidula*, *C. lavinia*, *C. lutea*, *C. natalensis*, *C. ontario*, *C. palloris*, *C.* nr. *punctipennis*, Australia spp. 1-2,5, Brazil spp. 1,3-4, Chile spp. 1-2, Mexico spp. 2-5, Nepal sp. 1, New Guinea spp. [numbered by Shima] 4,6,11,15,18, Peru sp. 1 and U.S. sp. 1. Examined published figures of: *C. bicolor* (Andersen 1983, fig. 23) and *C. pruinosa* (Shima 1970c, figs. 3f, 6).

Female genitalia (Figs. 149-150).— Short to relatively long and extensible. S_6 with short to average length hairs, though species with short hairs usually sparsely haired on most of sternite with longer row of hairs along posterior margin. T_6 varied from two small lateral sclerites to distinctly developed and narrowly discontinuous dorsally; spiracles of segment 6 near or enclosed within anteroventral portion of T_6. S_7 without anterior apodeme in most species, with apodeme in few; few species slightly to (rarely) sharply keeled posteromedially.

T_7 absent from few species, present as two small to large lateral sclerites in most species; spiracles of segment 7 in most species in membrane between segments 6 and 7, in few species enclosed within T_6 or near T_7. S_8 distinctly developed, haired. T_{10} absent to distinctly developed as a median plate or two sclerites.

Examined female genitalia of: *C. americana* complex, *C. bicolor* (Andersen 1983, fig. 10), *C. cornuta, C. lavinia, C. lutea, C. ontario*, Australia sp. 3 and Nepal sp. 4.

First instar (Figs. 157, 161-167).— Cephalopharyngeal skeleton: Labrum hatchet-like, though narrowly so in Nepal sp. 4 (Fig. 165); angled slightly downward in most species, oriented directly forward in Australia sp. 3 (Fig. 164). Lateral sclerite unmodified. Hypopharyngeal sclerite(s) unmodified. Both dorsal and ventral cornua present.

Posterior abdominal segments of first instar ventrally: Segment 7 bare or with tiny to distinct spinules posteriorly. Segment 8 with one to several rows of tiny to distinct spinules anteriorly; one to several rows of small to distinct, mostly uniform-sized spinules posteriorly. Segment 9 bare or with median group of spinules posteriorly; anus average-sized to large. Examined first instar of: two species of *C. americana* complex, *C. palloris*, Australia sp. 3, Brazil sp. 5, Chile sp. 1 and Nepal sp. 4.

Taxonomic changes

Lectotype designation for Ceromya cibdela (Vill.)

Ceromya cibdela was described in *Actia* by Villeneuve in 1913 from an unspecified number of specimens collected from Oshogbo, Nigeria, during October and November of 1910. While studying siphonine collections in the BMNH and CNC, I found a specimen in each labelled as the type of *C. cibdela* and bearing appropriate locality data. Each specimen bears a type label characteristic of the institution: a round, red-bordered "Type" label on the BMNH specimen, and a red, rectangular "TYPE" label on the CNC specimen (of the sort used in the CNC to denote types in the Mesnil collection). Both additionally have attached a Villeneuve determination label with the designation "Typ.". Both specimens fit Villeneuve's brief description of the species and by all indications are syntypes (no holotype designation was published). They are not, however, conspecific. The CNC specimen belongs to *Ceromya* and agrees with the current interpretation of *C. cibdela* (Mesnil 1954, 1963a, Crosskey 1976a), while the BMNH specimen belongs to *Siphona (Aphantorhaphopsis)*. To retain *C. cibdela* in its current usage I hereby designate the CNC specimen as lectotype. The condition of the CNC specimen also favors its selection as lectotype because it is a male in good condition while the BMNH specimen lacks its abdomen.

Notes about Ceromya fergusoni Bezzi and two related nominal species

Three named species of *Ceromya* from eastern Australia have flagellomere 1 bilobed: *C. fergusoni* (Bezzi 1923b; type-species of *Schizoceromyia*), *C. valida* (Curran 1927b; type-species of *Schizactiana*) and *C. invalida* (Malloch 1930a). These are unquestionably at least closely related, and as discussed below, perhaps conspecific. I dissected a male paratype (USNM) of *C. invalida*, and the presence of spinules distally on the membranous portion of the pregonite confirms its placement in *Ceromya s.s.*

As noted in Crosskey (1973: 137), the type of *C. fergusoni* is missing. Arnaud (1982) cites a paratype in MCSN, but this is in error. The MCSN specimen (examined by me in 1986) bears a collection label of "Sydney, 3.12.23 [December 3, 1923], Health Dept.", and stands in the MCSN collection under the label "*Schizotachina fergusoni* parat. Bezzi". Bezzi did not name a paratype, and his paper describing the species was read on November 28, 1923, about a week before the "paratype" was collected. The specimen is nonetheless important, for reasons given below.

Two characters given by previous authors separate *C. fergusoni, C. valida* and *C. invalida*. One is length of aristomere 2: in the description of *C. fergusoni* it is much longer than length of aristomere 3, in holotype of *C. valida* the articles are subequal in length, and in holotype of *C. invalida* it is slightly more than half length of aristomere 3. The second diagnostic character is presence or absence of an *ad* seta on mid tibia (character 24). *C. fergusoni* is cited as lacking this seta, it is long in the type of *C. valida* and short though stout in type of *C. invalida*. In all other respects the three named species seem not to differ significantly.

Malloch (1930a) knew about both Bezzi's *C. fergusoni* and Curran's *C. valida* when he described *C. invalida*, but finding Curran's description lacking information about the mid tibial *ad* seta, he divided all his material between *C. fergusoni* and *C. invalida*. Malloch apparently did not see any specimens with an aristomere 2 subequal in length to aristomere 3, as decribed for Curran's *C. valida*.[1]

I strongly suspect that the character states used to separate the three nominal species are unreliable within this species complex. Length of aristomere 2 is subject to some variation in some other siphonines, particularly those in which it is elongate. Under different circumstances, I would consider the mid tibial *ad* seta as reliable, but several factors suggest it may not be here. Firstly, Malloch's (1930a) specimen's of "*C. fergusoni*" and "*C. invalida*" were collected from the same locality (Sydney), and between the same months (Sept. to Dec.). Secondly, the MCSN specimen identified (by Bezzi?) as *C. fergusoni* lacks the mid tibial *ad* seta as described for that species, but has an aristomere 2 as described for *C. invalida* (also note that this specimen is labelled similarly to the specimens of "*C. fergusoni*" and "*C. invalida*" studied by Malloch). Thirdly, the types of the three nominal species vary in relative length of the mid tibial *ad* seta, suggesting a pattern of intraspecific variability. Fourthly, a BMNH specimen from South Australia has an aristomere two 0.8X length of aristomere 3 and a long mid tibial *ad* seta, placing it closest to *C. valida*, or by Malloch's criteria in *C. invalida*.

I have not examined enough material to firmly establish the conspecificity of the three nominal species discussed above. Neither have I examined the male genitalia of specimens of all three forms to determine if there are genitalic differences among them. Also the correlation between aristomere 2 length and presence/absence of a mid tibial *ad* seta needs to be studied to determine if these characteristics are distributed as uniformly as suggested by Malloch. The evidence now available casts doubt on the correctness of recognizing all three named species as valid species, but I reserve any change in nomenclature until more specimens can be examined and my above concerns addressed.

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[1] The labelled holotype of *C. valida* agrees in all respects with its description, but was collected from Palmerston on Sept. 1908 by Lichtwardt, and not (as cited by Curran) collected from Palmerston in 1910 by Fred P. Dodd. There is no other indication that this specimen is not the one selected by Curran as holotype of this nominal species.

Hosts

Ceromya s.s. species mostly parasitize Macrolepidoptera, without apparent preference for a particular family (Table 2). A single record for a rearing from a tenthredinid for *Ceromya bicolor* (a common European species also recorded from the Arctiidae and Lasiocampidae) is, if accurate, the only known record of a siphonine parasitizing a hymenopteran.

Phylogenetics

Species of *Ceromya s.s.* are not known to possess any synapotypic character states externally. The group, in addition to members of the *C. silacea* species group, is defined externally by the lack of derived features found in other siphonine lineages (see Recognition section of *Ceromya s.l.*), and *Ceromya s.s.* species are only separable from species of the *C. silacea* species group by features of the male genitalia.

Though members of *Ceromya s.s.* do not share known synapotypies externally, one derived characteristic of the male genitalia suggests the group is monophyletic, *i.e.* the more or less enlarged membranous area on the anterior surface of the pregonite, which in most *Ceromya s.s.* species is partially covered with tiny spinules (Figs. 39-40 and 77-83; in some species these spinules are only visible at magnifications of 100X-400X). These spinules are a derived state within the Siphonini, and so far as known are only present in *Ceromya s.s.* species and *Goniocera io*. The phylogenetic significance of this apotypic state in *G. io* is discussed in the Evolution chapter, though for the purposes of this discussion the state is interpreted as independently derived in *G. io* and *Ceromya s.s.*

The size and number of spinules on the pregonite of *Ceromya s.s.* species varies from species to species, and entirely absent from few (*cf.* Figs. 77-83). Species which lack spinules are, with rare exceptions (as discussed below), assignable to species groups which possess them (for example, the pregonite is bare in *C. flaviceps* and spinulose in several closely related species), so presence of spinules is here interpreted as the groundplan condition, or an underlying synapotypy (as defined in Evolution chapter), of *Ceromya s.s.* Several *Ceromya s.s.* species show modification from the simple spinulose condition, such as New Guinea sp. 6 (Fig. 78) and Brazil sp. 3 (Fig. 82), but the pregonite of these species is traceable to the primitive condition through species with intermediate states. More specifically, the pregonite of certain species suggests that the ring-shaped pregonite of New Guinea sp. 6 is derivable from a bilobed pregonite of a *C. flaviceps*-like ancestor, and the enlarged spines on the pregonite of Brazil sp. 3 are derivable from an ancestor with a spinulose condition similar to Mexico sp. 5 (Fig. 81; note that the spined condition of the pregonite in Brazil sp. 3 is distinctly different from the *Actia*-type, Figs. 85-86).

The pregonite of *C. lutea* (Fig. 83) is unique in curving posteriorly. No other siphonine is known to share this condition, and along with the derived shapes of its male sternum 5 (Fig. 57) and distiphallus (Fig. 116), this seems to indicate that this species is not closely related to other known *Ceromya s.s.* species. *C. lutea* is interpreted as a member of *Ceromya s.s.* because it has tiny spinules on the anterior (membranous) portion of the pregonite.

Setulation of wing vein R_{4+5} is a markedly labile character within siphonine lineages (Table 1), though all *Ceromya s.l.* species except *C. cephalotes*, *C. natalensis* and *C. montrosicornis* have R_{4+5} setulose beyond *r-m*. The placement of these three species in *Ceromya* was carefully evaluated because the monophyly of *Ceromya s.l.* is not well established, and *Entomophaga* and *Proceromyia* species are also characterized by R_{4+5} not setulose beyond *r-m*. The male genitalia of *C. cephalotes* and *C. natalensis* were examined, and though spinules are absent from the pregonite, other features ~~of the male~~ genitalia indicate that the former belongs to the *C. bicolor* group and the latter is closely related to *C. languidula*. Both species are therefore retained in *Ceromya s.s.* The placement of *C. monstrosicornis* in *Ceromya s.s.* is more equivocal because the male genitalia were unavailable for study and for other reasons discussed below.

Stein described *C. monstrosicornis* in 1924 in a new monobasic genus, *Stenoparia*. Mesnil (1963a) classified *Stenoparia* as a subgenus of *Ceromya*, adding *C. nigrohalterata* to the taxon. Species of *C. (Stenoparia)* and *C. (Proceromyia)* were separated from those of *Ceromya s.s.* by not having wing vein R_{4+5} setulose beyond crossvein *r-m*, and the latter (with single species *C. macronychia*) was separated from the former by its larger tarsal claws and several other minor differences (1963a: 829). In the classification adopted here, *C. macronychia* and *Nipponoceromyia pubioculata* (described after Mesnil's Palearctic revision) are included in the genus *Proceromyia*, and *C. nigrohalterata* is included in the genus *Entomophaga* with *E. exoleta* (see Phylogenetics sections of *Proceromyia* and *Entomophaga*).

There is insufficient evidence to place *C. monstrosicornis* in *Entomophaga* or *Proceromyia* (it certainly is not a *Goniocera* species). This species lacks the elongate aristomere 1 of *Entomophaga* or large tarsal claws of *Proceromyia*, and does not have a long preapical *ad* seta on the fore tibia which is common to both. Yet *C. monstrosicornis* is the only *Ceromya s.l.* species with a bare prosternum (as in *Proceromyia*), one of only three *Ceromya s.l.* species with R_{4+5} not setulose beyond *r-m*, and has a dark, uniformly pruinose abdomen as in *Entomophaga* and *Proceromyia*. Unfortunately, a male specimen of *C. monstrosicornis* could not be located in North American or European collections (and the male type could not be located in the ZMHU), so the phylogenetically important characters of the male genitalia could not be studied. *C. monstrosicornis* is left in *Ceromya s.s.* (not in *Ceromya s.l.*, as it is certainly not a member of the *C. silacea* sp. grp.) until its male genitalia are studied and its relationship to *Ceromya*, *Entomophaga* and *Proceromyia* established. Though *C. monstrosicornis* shares a haired parafacial and uniformly pruinose abdomen with *Goniocera* species, other differences preclude a close relationship between these taxa.

The placement of two undescribed species, Australia sp. 3 and Nepal sp. 1, in *Ceromya s.s.* also requires explanation. These species differ from other *Ceromya s.l.* species in having a long preapical *ad* seta on the fore tibia. They share this state with *Entomophaga* and *Proceromyia* species and some species of *Goniocera* and *Actia*, so the phylogenetic interpretation of this state in these *Ceromya* species is relevant to their placement. These species are certainly not close to *Actia*, so the discussion which follows focuses on their possible affinities with the other three genera.

Australia sp. 3 is known only from adult females and first instars, so pertinent characters of the male genitalia are unknown. Females of this species are unusual among *Ceromya* species in having enlarged tarsomere 5 on all legs and a sharply keeled sternum 7, while the first instar has an uncharacteristically broad labrum (Fig. 164). These states are evidently autapotypies as they are not shared with the non-*Ceromya* genera mentioned above. External characteristics of the female favour the placement of Australia sp. 3 in *Ceromya s.s.*, though it is noted that examination of the male genitalia would provide valuable information about this species' affinities.

The placement of Nepal sp. 1 is enigmatic, as it has a haired parafacial (with several larger setulae) in common with all but one *Goniocera* species (though parafacial more heavily setulose in those species than in Nepal sp. 1; Fig. 1), *Proceromyia pubioculata* and *Ceromya monstrosicornis* (both with hairs only on parafacial; Fig. 3), long preapical *ad* seta on fore tibia (as mentioned above), haired prosternum (shared with most siphonines, but not *Proceromyia* and some *Goniocera* species), R_{4+5} setulose beyond *r-m* (as in *Goniocera* species and almost all *Ceromya* species, but not *Entomophaga* and *Proceromyia* species), and uniformly pruinose abdomen (as in *Goniocera*, *Proceromyia* and *Entomophaga* species, and *C. monstrosicornis* but not other *Ceromya* species). The male genitalia of Nepal sp. 1 do not closely resemble those of the above non-*Ceromya* genera, but similarly lack the typical spinules on the pregonite possessed by most *Ceromya s.s.* species (male genitalia of *C. monstrosicornis* unavailable for study) and has an aedeagus which cannot be placed into a *Ceromya s.s.* species group (though very different from the typical shape in the *Ceromya silacea* species group). In view of these genitalic differences a close relationship with *Goniocera* species is unlike, as Nepal sp. 1 also lacks a row of *ad* setae on the mid tibia (synapotypic of *Goniocera* species).

Such an array of character states in Nepal sp. 1 is not easily interpretable, and any placement at this time is tentative at best. This species seems to share more states with species of *Ceromya s.s.* than with species of the other genera discussed, so is placed here for the present. A possible relationship with *C. monstrosicornis* needs to be investigated.

Geographic distribution

Thirty-nine described species are assigned to *Ceromya s.s.*, of which only eight are New World in distribution (see Sabrosky and Arnaud 1965 for ranges of species north of Mexico, Guimarães 1971, Cortés 1967, and Cortés and Hichins 1969 for ranges of species south of the United States). However, preliminary study of specimens of New World *Ceromya s.s.* indicates that the number of described species is a significant underestimate of the true diversity of the group in the New World. I estimate from examined material that there are about 15 undescribed New World species, almost all Neotropical in distribution.

Most accurately known are the British (Crosskey 1976b) and European (Draber-Mońko 1981, Herting 1984) faunas, consisting of five described species. A key for recognition of all of these species has not been published, though they are treated in part in Mesnil (1963a) and Herting (1977). The fauna of Asia is less well documented, and appears to be very depauperate. *C. bicolor* is the only *Ceromya s.s.* species recorded from central Asia (Richter 1971, 1975, 1980), and the only other described eastern Palearctic species, *C. pruinosa*, is apparently restricted to Japan (though Herting 1984 cites this species as a possible synonym of *C. bicolor*). However, I have seen specimens of several undescribed species of *Ceromya s.s.* collected from Nepal.

Greatest diversity of described *Ceromya s.s.* species in the Old World is recorded from the tropics: eight species in the Afrotropical region and 13 in the Oriental region (distributions given in Crosskey 1980, 1976a, respectively; key to Philippine species in Dear and Crosskey 1982, though these authors include *S. (Aphantorhaphopsis)* in their concept of *Ceromya*). Only three species are described from Australia (Crosskey 1973). Still, the described portion of the Old World fauna of *Ceromya s.s.* belies its true diversity: Shima (pers. comm.) has tentatively recognized close to 20 new species in the Oriental region, and I have seen specimens of numerous undescribed species from Australia and Africa.

From a cosmopolitan perspective *Ceromya s.s.* can best be considered a tropical group, with relatively few species in the Nearctic and Palearctic regions. The genus still requires a great deal of descriptive work, especially with respect to its tropical elements, before it is adequately known.

List of described species included in Ceromya sensu stricto

S *amblycera* (Aldrich), 1934: 132 (*Actia*). Holotype male, Argentina: Bariloche (USNM). Holotype examined. **New combination**, moved from *Actia*.

N *americana* (Townsend), 1892: 69 (*Thryptocera*). Holotype male (not female), USA: D.C., Washington (UKL). Holotype examined.

syn. *elyii* (Walton), 1914: 91 (*Polychaetoneura*). Three female syntypes, USA: Connecticut, East River (USNM).— Curran, 1933a: 5. Syntypes examined.

A *amicula* Mesnil, 1954: 40. Holotype male, Zaire: Bambesa (MRAC). Holotype examined.

O *apicipunctata* (Malloch), 1926: 510 (*Actia*). Holotype male, Philippines: Luzon, Benquet (USNM). Holotype examined.

O *bellina* Mesnil, 1957: 44. Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

P *bicolor* (Meigen), 1824: 354 (*Tachina*). Holotype male, no locality data (MNHN).

syn. *fasciata* (Stein), 1924: 132 (*Actia*). Lectotype female (by designation of Herting, 1977: 10), Yugoslavia: Sarajevo (NMBA).— Considered a possible color variant of *bicolor* Mg. by Herting, 1977: 10.

rufina (Zetterstedt), 1838: 641 (*Tachina*). Holotype female, Sweden: Dalecarlia (UZI).— Herting, 1984: 121.

testacea Robineau-Desvoidy, 1830: 88. Type(s), France: Lille (lost).— Herting, 1974: 18.

A *buccalis* (Curran), 1933c: 163 (*Actia*). Holotype male, Zimbabwe: Gatooma (AMNH). Holotype examined.

O *capitata* Mesnil, 1957: 42. Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

O *cephalotes* Mesnil, 1957: 40. Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

A *cibdela* (Villeneuve), 1913: 35 (*Actia*). Lectotype male **(by designation in text)**, Nigeria: Oshogbo (CNC). Lectotype examined.

syn. *cibdella*. Mispelled reference to *cibdela* Villeneuve (Curran, 1927a: 323).

S *cornuta* (Aldrich), 1934: 131 (*Actia*). Holotype male, Chile: Angol (USNM). Holotype examined. **New combination**, moved from *Actia*.

P *dilecta* Herting, 1977: 10. Holotype male, Switzerland: Gordola (SMNS). Holotype examined.

O *dubia* (Malloch), 1930b: 146 (*Actia*). Holotype female, Malaysia: Selangor (BMNH). Holotype examined.

A *femorata* Mesnil, 1954: 38. Holotype male, Zaire: Bambesa (MRAC). Holotype examined.

U *fergusoni* (Bezzi), 1923b: 657 (*Schizotachina*). Holotype male, Australia: New South Wales, Sydney (type missing according to Crosskey, 1973: 137).

syn. *fergussoni*. Mispelled reference to *fergusoni* Bezzi (Curran, 1927b: 355-356).

P *flaviceps* (Ratzeburg), 1844: 172 (*Musca* (*Tachina*)). Type, Germany (lost).

syn. *flaviceps* (Stein), 1924: 134 (*Actia*).— Objective synonym; see Herting, 1982: 8 and 1984: 190 (note 94), *cf.* Herting, 1977: 9.

P *flaviseta* (Villeneuve), 1921: 45 (*Actia*). Male syntype from Berlin, Germany, female syntype from Samara, USSR (CNC). Syntypes examined.

O *hirticeps* (Malloch), 1930b: 146 (*Actia* (*Pseudactia*)). Holotype male, Malaysia: Kedah Peak (BMNH). Holotype examined.

U *invalida* (Malloch), 1930a: 305 (*Actia* (*Schizoceromyia*)). Holotype male, Australia: New South Wales, Sydney (SPHTM). Holotype examined.

A *languidula* (Villeneuve), 1913: 36 (*Actia*). Two male syntypes, Nigeria: Oshogbo (BMNH and CNC). Syntypes examined.

A *languidulina* Mesnil, 1977b: 178. Holotype female, Madagascar: Ambohitantely (MNHN).

O *latipalpis* (Malloch), 1930b: 145 (*Actia*). Holotype female, Malaysia: Kedah Peak

(BMNH). Holotype examined.

A *lavinia* (Curran), 1927a: 324 (*Actia*). Holotype female, South Africa: Natal, Clan Syndicate (PPRI). Holotype examined.

O *longimana* Mesnil, 1957: 38. Holotype female, Burma: Kambaiti (ZMU). Holotype examined.

S *lutea* (Townsend), 1927: 283 (*Actinactia*). Holotype male, Brazil: São Paulo (USNM). Holotype examined. **New combination.**

A *luteicornis* (Curran), 1933c: 162 (*Actia*). Holotype male, southern Zimbabwe (BMNH). Holotype examined.

O *maculipennis* (Malloch), 1930b: 141 (*Actia*). Holotype male, Malaysia: Selangor (BMNH). Holotype examined.

P *monstrosicornis* (Stein), 1924: 128 (*Stenoparia*). Holotype male, German Democratic Republic: Mecklenburg (ZMHU; not located, maybe lost).

syn. *monstruosicornis*. Mispelled reference to *monstrosicornis* Stein (Mesnil, 1963a: 829, 831).

A *natalensis* (Curran), 1927a: 325 (*Actia*). Holotype male, South Africa: Natal, Cramond (PPRI). Holotype examined.

N *ontario* (Curran), 1933a: 4 (*Actia*). Holotype female, Canada: Ontario, Lake of Bays, Norway Point (CNC). Holotype examined.

N *palloris* (Coquillett), 1895b: 50 (*Lasioneura*). Lectotype male (by designation of Coquillett, 1897: 58), USA: New Hampshire (USNM). Lectotype examined.

O *portentosa* Mesnil, 1957: 43. Holotype female, Burma: Kambaiti (ZMU). Holotype examined.

P *pruinosa* Shima, 1970c: 188. Holotype male, Japan: Hokkaido, Berabonai (BLKU). Paratype examined.

O *punctipennis* (Malloch), 1930b: 140 (*Actia*). Holotype male, Malaysia: Kedah Peak (BMNH). Holotype examined.

O *punctum* (Mesnil), 1953: 107 (*Actia*). Holotype male, China: Canton (BMNH).

Holotype examined.

O *rotundicornis* (Malloch), 1930b: 145 (*Actia*). Holotype male, Malaysia: Pahang, Fraser's Hill (BMNH). Holotype examined.

S *subopaca* (Aldrich), 1934: 133 (*Actia*). Holotype male, Argentina: Bariloche (BMNH). Holotype examined.

S *unicolor* (Aldrich), 1934: 133 (*Actia*). Holotype male, Argentina: Bariloche (BMNH). Holotype examined.

U *valida* (Curran), 1927b: 356 (*Actia* (*Schizactiana*)). Holotype male, Australia: Queensland, Palmerston (DEI). Holotype examined.

Nomen dubium

P *erythrocera* Robineau-Desvoidy, 1830: 87. Type(s), France (lost).

4.11 Ceromya silacea (Meigen) species group

Figs. 35, 37, 52, 84, 112, 148, 160.

Recognition

Male genitalic features provide the only characteristics by which members of the *Ceromya silacea* species group (a strictly Old World taxon) can be distinguished from *Ceromya s.s.* species. Species of *C. silacea* species group are unique within the Siphonini in possessing posteriorly on the distiphallus an infolded and sclerotized structure (Fig. 112) - in other siphonines the posterior margin is sclerotized or membranous (the latter in all but very few species), but not infolded.

Ceromya silacea is one of the species with greatest development of the infolded structure on the distiphallus. As shown in Fig. 112, this structure is extended anteriorly to near the anterior margin of the distiphallus (note too that the distiphallus is extensively membranous anteriorly and laterally in this species) and projects posteriorly from between the posterolateral margins. In some other species of this species group the infolded structure is smaller; in *C. languidula* it is virtually undeveloped.

The pregonite of species of *C. silacea* species group is long and sickle-like in most species (Fig. 84) and shorter and apically rounded in others - the membranous portion is not expanded and spinules are absent (*cf. Ceromya s.s.* section and Figs. 39-40, 77-83).

Description

Length: 3.0-5.5mm.

Head.— Five frontal setae in most species, three (*C. silacea*) or four in very few; normal arrangement. Anterior proclinate orbital seta longer than posterior one. Eye size of male medium-large to large, 0.77-0.86 head height; size in female subequal to that of male. Flagellomere 1 of male medium-short to medium length, 0.47-0.56 head height; shape from linear to large and almost triangular, not bifid. Flagellomere 1 of female smaller than in male. Aristomere 1 short. Aristomere two 1.5-5X longer than wide. Aristomere 3 rather short to long and evenly tapered; micropubescent to pubescent. Clypeus U-shaped. Palpus short, clavate. Proboscis with prementum short, labella padlike.

Thorax (Figs. 35, 37).— Prosternum setulose. Lower proepimeral seta weak, not directed downward. Katepisternum bare anterior to mid coxa. Lower katepisternal seta much shorter than upper anterior seta in most species, subequal in length to it in three closely related species: *C. normula, C. similata* and *C. varichaeta*. Three or four postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Mid femur with pilose patch on anterior surface from about midlength to distal end in males of *C. normula* and *C. varichaeta* (Fig. 35). Tarsomeres normal in size, claws small. Wing: CuA_1 with distal portion 0.29-0.47X length of proximal portion (mean 0.36); anal vein not extended to wing margin. Wing setulae: R_1 dorsally bare, or distally or entirely setulose, ventrally bare or distally setulose; R_{4+5} setulose from base to beyond *r-m*; CuA_1 bare or setulose.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae; lateral marginal setae absent to strong. T_3-T_5 average or with weak lateral discal setae.

Male genitalia (Figs. 52, 84, 112).— S_5 with, inner (or posterior) margins of processes obtusely angled to almost transverse (Fig. 52 and Shima 1970c, figs. 3d,e); apical lobe undifferentiated to rounded; median lobe rounded or pointed in most species, slightly flattened medially in C. *varichaeta* (but not to degree found in *Goniocera*); without accessory lobe; processes very sparsely setulose (most species) to densely setulose (*C. varichaeta*). T_6 present as pair of small lateral sclerites. Ejaculatory apodeme with fan-shaped portion half to subequal width of hypandrial apodeme. Pregonite in profile long and sickle-like in most species (Fig. 84), apically rounded in *C. varichaeta*; bare. Epiphallus absent from most species, present in *C. varichaeta*. Distiphallus (Fig. 112) broad in profile, with short to long posterolateral arm except in *C. varichaeta*, and unique infolded and sclerotized structure formed from posterior surface (large in most species, very small in *C. varichaeta*) which is deeply U-shaped in posterior view. Postgonite large, apically bilobed. Surstylus average length to long, straight in few species (*e.g.* Shima 1970c, fig. 5b), thin and curved posteriorly in most (*e.g.*, *op. cit.*, fig. 5a); with long hairs along length in *C. varichaeta* (also found in *C. languidula* of *Ceromya s.s.*); basally fused with epandrium or free (*C. varichaeta*). Cerci rather short to average length, posteriorly deeply inflexed at midlength (*e.g.*, *op. cit.*, fig. 5b) to gently curved or almost straight (*e.g.*, *op. cit.*, fig. 5a); moderately to densely setose on basal half.

Examined male genitalia of: *C. mellini*, *C. silacea*, *C. varichaeta*, Australia sp. 4 and Nepal sp. 2. Examined published figures of: *C. dorsigera* and *C. silacea* (both in Shima 1970c, figs. 3d,e, 5).

Female genitalia (Fig. 148).— (Only *C. silacea* examined.) Medium length (slightly extensible). S_6 with average length hairs. T_6 present as two lateral sclerites; enclosing spiracles of segment 6 in anteroventral portion. S_7 with anterior apodeme; without posteromedial keel. T_7 present as two lateral sclerites; spiracles of segment 7 enclosed within anterior portion of T_7. S_8 distinctly developed, haired. T_{10} present as two distinct sclerites.

Examined female genitalia of: *C. silacea*.

First instar (Fig. 160).— Cephalopharyngeal skeleton: Labrum hook-like. Lateral sclerite triangular, with slender projection anteriorly. Hypopharyngeal sclerite unmodified. Both dorsal and ventral cornua present, though dorsal cornu relatively short.

Posterior abdominal segments of first instar ventrally: Segment 7 bare. Segment 8 with two rows of small ~~spinules~~ anteriorly; about five even rows of spinules posteriorly, graded in size from small spinules in anterior row to large spinules in posterior row. Segment 9 with row of large spinules posteriorly; anus average-sized.

Examined first instar of: *C. silacea*.

Taxonomic changes

Status of Ceromya similata Mesnil

Mesnil described *Ceromya similata* in 1954 as a sympatric subspecies of *C. varichaeta* (Curran), noting that it differs from the nominal subspecies primarily in having R_1 distally rather than entirely setulose dorsally. As explained elsewhere (*e.g.* Taxonomic changes section of *Siphona (Siphona)*), I do not accept the concept of sympatric subspecies; therefore, *C. varichaeta similata* must either be elevated to species status or declared conspecific with *C. varichaeta*.

I have examined the holotypes of *C. varichaeta* and *C. similata*, and a closely related species *C. normula* (the latter placed in *Peribaea* by Crosskey, 1980). *C. varichaeta* and *C. normula* are based on males which share a striking synapotypy: a pilose patch anteriorly on the mid femur (Fig. 35). The types differ little except that R_1 is dorsally setulose entirely in *C. varichaeta* and only distally in *C. normula*. This difference in R_1 setulation is very reliable as a species specific character (in contrast to the states R_1 distally bare or setulose), so I accept *C. varichaeta* and *C. normula* as valid species. Setulation of R_1 in the holotype of *C. similata* matches that of *C. normula*, not *C. varichaeta*, and might be conspecific with that species. However, the type of *C. similata* is female (thus lacking the male-linked pilose patch on mid femur), so is difficult to compare critically with the male types of the other two nominal species. Though *C. similata* has been associated with *C. varichaeta* in publications, it is more likely conspecific with *C. normula* or a valid species. I treat *C. similata* here as a valid species pending examination of additional male and female specimens of the three nominal species.

Hosts

Hosts have only been recorded for two species, and both belong to the Noctuidae (Table 2).

Phylogenetics

Adults of the *C. silacea* species group are similar to those of *Ceromya s.s.* externally, but differ in two important male genitalic characteristics. First, they lack spinules on the membranous anterior portion of the pregonite, and second have a uniquely infolded posterior margin on the distiphallus (Fig. 112). The first characteristic is interpreted as synapotypic of *Ceromya s.s.*, the second synapotypic of the *C. silacea* species group (monophyly of *Ceromya s.l.* discussed in Evolution chapter).

In *C. silacea, C. mellini*, Australia sp. 4 and Nepal sp. 2, the infolded region of the distiphallus is very large (Fig. 112). In *C. varichaeta* the infolded region is small and nearer the apex, and perhaps represents a more primitive condition. The male genitalia of the other species here placed in this group were not examined, but these species are thought to belong here because they appear very similar externally to certain well established members of this group.

The labrum is hook-like in the first instar of *C. silacea* and hatchet-like or intermediate in other examined *Ceromya s.l.* species. It remains to be determined whether this feature is another synapotypy of the *C. silacea* species group.

Geographic distribution

The eight described species of the *Ceromya silacea* species group are exclusively Old World in distribution. The centre of diversity is the Old World tropics (see Crosskey 1976a and 1980 for ranges of Oriental and Afrotropical species; none described from Australia), with only three species recorded from the Palearctic region: *C. dorsigera* (described from Switzerland and recorded from Japan by Shima 1970c), *C. silacea* (widespread, with records from England (Crosskey 1976b), Eurasia (Mesnil 1963a, Shima 1970c, Richter 1971, 1976b, 1980, Draber-Mońko 1981), and southern India (examined specimens from CNC)), and *C.*

pendleburyi (SE Asia and Japan, Mesnil 1963a and Shima 1970c). The three Palearctic species are keyed in Shima (1970c). In addition to the described species I have seen specimens of a new species from Nepal (Nepal sp. 2) and another from Australia (Australia sp. 4) [numbers used here for new species refer to *Ceromya s.l.*].

List of described species included in Ceromya silacea species group

P *dorsigera* Herting, 1967a: 8. Holotype male, Switzerland: Gordola (SMNS). Holotype examined.

O *mellina* (Mesnil), 1953: 109 (*Actia*). Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

A *normula* (Curran), 1927a: 322 (*Actia*). Holotype male, South Africa: East London (PPRI). Holotype examined. **New combination**, moved from *Actia*.

O *patellicornis* Mesnil, 1957: 40. Holotype male, India: Darjeeling (BMNH). Holotype examined.

O,P *pendleburyi* (Malloch) 1930b: 144 (*Actia*). Holotype male, Malaysia: Pahang (BMNH). Holotype examined.

O,P *silacea* (Meigen), 1824: 355 (*Tachina*). Holotype male, no locality data (MNHN).

syn. *siebeckii* (Sintenis), 1897: 151 (*Thryptocera*). Holotype female, Estonia: Pärnu (not located).— Herting, 1984: 121.

A *similata* Mesnil, 1954: 39 (as subspecies of *Ceromya varichaeta* (Curran)). Holotype female, Zaire: Tshumba (MRAC). Holotype examined. **New status.**

A *varichaeta* (Curran), 1927c: 6 (*Actia*). Holotype male, Zaire: Faradje (AMNH). Holotype examined.

4.12 Actia Robineau-Desvoidy

Figs. 8-10, 21, 23, 29, 31, 33, 41-42, 58-59, 85-86, 117-119, 151-152, 168-171.

Actia Robineau-Desvoidy, 1830: 85. The I.C.Z.N. has been requested by O'Hara (1985) to designate *Roeselia lamia* Meigen as type species of *Actia* R.-D. The request conforms to current usage, so *R. lamia* is used here as type species pending a decision by the I.C.Z.N.

Thryptocera Macquart, 1834: 310. Type-species, *T. bicolor* Macquart, 1834 (by designation of Townsend, 1916: 624) = *Tachina crassicornis* Meigen, 1824.— Herting, 1976: 3.

Tryptocera. Variant spelling of *Thryptocera*.

Gymnophthalma Lioy, 1864: 1341. Type-species, *Tachina crassicornis* Meigen, 1824 (monotypy).

Gymnopareia Brauer and Bergenstamm, 1889: 103 (35). Type-species, *Tachina crassicornis* Meigen, 1824 (monotypy).

Gymnoparia. Variant spelling of *Gymnopareia*.

Actiopsis Townsend, 1917: 121. Type-species, *A. autumnalis* Townsend, 1917 (original designation).

Setasiphona Townsend, 1934: 248. Type-species, *Actia siphonosoma* Malloch, 1930 (original designation).

Recognition

Actia is a diverse genus of cosmopolitan distribution. With few exceptions, members are recognized externally by the presence of a row of hairs on the katepisternum anterior to the mid coxa (*cf.* Figs. 33 and 34). Among other siphonines, only the European species *Entomophaga exoleta* shares this state, and is distinguished from *Actia* by its elongate aristomere 1 (Fig. 4), long preapical *ad* seta on fore tibia, and features of the male genitalia (especially sternum 5 - *cf.* Figs. 50 and 58-59). Five *Actia* species, *A. completa* and *A. magnicornis* from Malaysia and *A. parviseta*, *A.* nr. *parviseta* and Australia sp. 5 from eastern Australia, either lack this row of katepisternal hairs or the number of hairs is reduced. These species have two setulae on the upper portion of the anepisternum (see below), and males are additionally recognized as members of *Actia* by their V-shaped sternum 5 (similar to Figs. 58-59) and spined pregonite (similar to Figs. 85-86).

The upper portion of the anepisternum has two setulae in almost all *Actia* species (Fig. 31; one setula in most other siphonines, Fig. 32). Two setulae are present in few *Peribaea* species and few species in different *Siphona s.l.* lineages, but this state seems to be restricted to *Actia* among siphonines in which the anal vein does not extend to the wing margin (Table 1).

Three *Actia* species, *A. completa* and *A. fulvicauda* from Malaysia and *A. chrysocera* from the Seychelles Islands, are the only known siphonines other than *Peribaea* and *Siphona s.l.* species to have the anal vein extended to the wing margin. *A. fulvicauda* and *A. chrysocera* possess a row of katepisternal hairs as in most other *Actia* species, but *A. completa* has an incomplete row. *A. completa* is recognized as an *Actia* species by its two anepisternal setae and *Actia*-like male genitalia (see above).

Males of most *Actia* species have a more or less V-shaped sternum 5, with little or no constriction of the median lobes above the median cleft (Figs. 58-59). Sternum 5 departs slightly from this shape in few species, but even in these it more closely resembles the sternum 5 of other *Actia* species than non-congeneric siphonines.

The only feature possibly universal among *Actia* species is a J-shaped, spinose pregonite (Figs. 41-42 and 85-86). All examined male genitalia of *Actia* species were of this type, including species mentioned above as having atypical external features.

Description

Length: 2.5-6.0mm.

Head (Figs. 8-10).— Five frontal setae (rarely four), normal arrangement. Anterior proclinate orbital seta longer than posterior one in almost all species. Eye of male small to large, 0.65-0.89 head height; eye of female subequal to or slightly smaller than in male. Flagellomere 1 of male markedly varied in length, 0.43-0.75 head height; linear to broad; bifid in only one known species, *A. yasumatsui* (Shima 1970b, fig. 1). Flagellomere 1 of female smaller than in male or subequal in size; not bifid. Aristomere 1 short. Aristomere 2 varied from 1.5-5X longer than wide, relatively short (2-3X) in most species. Aristomere 3 short and thickened to near tip, to long and evenly tapered; almost bare to short plumose. Clypeus varied from narrow and enclosed in membrane to broadened or U-shaped. Palpus short in most species, long in some species with elongate proboscis; enlarged apically in females of few species; clavate. Prementum short to long, in few Old World species of latter slender and elongate like typical *Siphona* species (Fig. 9). Labella also markedly varied, padlike or slightly lengthened (like in *Siphonopsis*) in most species, quite elongate (half head height or longer) and with numerous pseudotracheae and flexible in life in few species (*e.g. A. fallax, A. jocularis, A. longilingua*); in very few Old World species labella as in *Siphona* species (Fig. 9): about head height in length, basal portion inflexible in life, with reduced number of pseudotracheae apically (*e.g. A. malaisei).*

Thorax (Figs. 21, 23, 29, 31, 33).— Prosternum setulose in almost all species (apparently bare only in *A. nigra*). Lower proepimeral seta weak or absent. Most species with row of hairs on katepisternum directly anterior to mid coxa extended upward almost to lower katepisternal seta (Fig. 33); several hairs in lower corner only (*i.e.* groundplan condition of Siphonini) in *A. parviseta* and *A.* nr. *parviseta*, and several hairs in lower corner to row extended halfway to lower katepisternal in *A. completa, A. magnicornis* and Australia sp. 5. Lower katepisternal seta shorter (in most species much shorter) than upper anterior seta (Fig. 31). Four postsutural dorsocentral setae in most species, three in few. Upper part of anepisternum with two setulae in most species (Fig. 31), with single setula in very few. Fore tibia with preapical *ad* seta much shorter than *d* seta in most species, ranging to about 0.75 length of *d* seta in few species (known in *A. infantula, A. lamia* and *A. nudibasis*), and subequal to *d* seta in few species (known in *A. eucosmae, A. nigriventris, A. parviseta*, and several undescribed Australian species). Mid tibia with one *ad* seta in almost all species (markedly reduced or absent from *A. eucosmae, A. parviseta, A. perdita* and Australia sp. 3). Tarsomeres normal in size, or tarsomere 5 of fore leg broadened (known only in female of *A. tarsata*, though slightly larger than average in females of few other species), tarsomere 5 of all legs slightly enlarged in female of *A. nigriventris*; claws short. Wing (Fig. 21) with vein *M* complete in most species, slightly developed or absent after bend in some (*e.g. A eucosmae, A. exsecta, A. lamia, A. munroi, A. nigriventris, A. perdita, A. pulex, A. rufescens* and *A. takanoi*); vein CuA_1 with distal portion 0.25-1.6X length of proximal portion (in most species short, 0.3-0.7; mean 0.56); anal vein not extended to wing margin, except in *A. completa, A. fulvicauda* and faintly in *A. chysocera*. Wing setulae: R_1 dorsally bare, or distally or entirely setulose, ventrally bare or distally setulose; R_{4+5} setulose from base to or beyond *r-m*; CuA_1 bare or setulose; unusual patterns in few species with additional veins setulose: *A. ciligera* (R_{2+3}, R_{4+5} and *M* setulose dorsally and ventrally) *A. fallax* (*M* setulose ventrally) and *A. gratiosa* (*Sc* setulose dorsally).

Abdominal terga 1-5.— Abdomen ovoid in shape in most species, slightly elongate in very few. T_{1+2} without median marginal setae; lateral marginal setae absent from most species, strong in few. T_3-T_5 average in most species, with weak lateral discal setae in few (particularly among species in Holarctic region).

Male genitalia (Figs. 41-42, 58-59, 85-86, 117-119).— S_5 little varied, processes elongate, rounded or pointed posteriorly, inner margins approximately V-shaped in most species (Fig. 58), obtusely angled in very few (Fig. 59; rarely as much as in other siphonines); median lobe undifferentiated (Fig. 58) or scarcely differentiated (Fig. 59); median cleft scarcely constricted posteriorly by median lobes in most species (Fig. 58), distinctly constricted by rounded (Fig. 59) to elongate median lobes in few; processes moderately setulose with several pair of large setae. T_6 slightly sclerotized, generally continuous dorsally. Ejaculatory apodeme varied from small to very large (0.5-2.0X width of hypandrial apodeme), in most species width of fan-shaped portion subequal to width of hypandrial apodeme. Pregonite (Figs. 85-86) broad subapically and approximately J-shaped, outer surface short spinose on apical half or less; asetose. Epiphallus absent. Distiphallus (Figs. 117-119) with posterior margin partially developed in some species, absent from others; not laterally broadened as in *Peribaea* species; in profile from broad and truncate apically to very narrow and sharply pointed apically (Fig. 119), with numerous forms between. Postgonite in most species apically broad, rounded or truncate, in few species narrow or intermediate in width. Surstylus short to long, shape varied relatively little, narrow or broad in a few species, intermediate in most; medium to long hairs basally in some species of an Old World group; basally free from epandrium. Cerci varied little, short to average length, sharply inflexed at midlength in some species, smoothly curved posteriorly in most; moderately setose on basal half.

Examined male genitalia of: *A. autumnalis, A. brevis, A. completa, A. diffidens, A. infantula, A. interrupta, A. lamia, A. longilingua, A. magnicornis, A. malaisei, A. nitidella, A. nudibasis, A. parviseta, A. pilipennis, A. rufescens*, Australia spp. 1-2,4-5, Jamaica sp. 1, Liberia sp. 1, Mexico sp. 1, Nepal spp. 1-2, New World spp. 1-19 and Uganda sp. 1. Examined published figures of: *A. lamia* (Andersen 1983, fig. 25), *A. darwini, A. painei* (both in Crosskey 1962, figs. 1-6), *A. jocularis, A. nigra* (both in Shima 1970c, figs. 2, 3b,c, 4), *A. pokkarana* and *A. yasumatsui* (both in Shima 1970b, fig. 2).

Female genitalia (Figs. 151-152).— Short and markedly uniform and unspecialized, with only minor differences among species. S_6 with average length hairs. Spiracles of segment 6 enclosed in T_6; in some species T_6 forming a broad sclerite narrowly discontinuous dorsally, in others represented by two small lateral sclerites, in few species unsclerotized. S_7 without anterior apodeme except for short projection in *A. crassicornis* (Andersen 1983, fig. 12); without posteromedial keel. T_7 absent or present only as two small lateral sclerites; spiracles of segment 7 in membrane between segments 6 and 7. S_8 distinctly developed, haired, with lateral edges curved inward. T_{10} distinctly developed as median sclerite, in most species subequal in size to S_8.

Examined female genitalia of: *A. diffidens, A. interrupta, A. lamia, A. malaisei, A.* nr. *parviseta*, Australia sp. 1, New World spp. 4-5 and Zaire sp. 1. Examined published figures of: *A. crassicornis* and *A. lamia* (both in Andersen 1983, figs. 11, 12).

First instar (Figs. 168-171).— Cephalopharyngeal skeleton: Labrum hatchet-like; angled slightly downward. Lateral sclerite unmodified. Hypopharyngeal sclerite small. Dorsal cornu absent and ventral cornu shortened. [Farinets (1980, figs. 30-31) illustrated the first instar of *Actia dubitata*, showing distinct dorsal and ventral cornua. I have not studied the first instar of this species, but all eight *Actia* species here described lack a dorsal cornu, so I am uncertain about the accuracy of Farinet's findings. Perhaps his depiction of *A. dubitata* with unshaded dorsal and ventral cornua is an indication that these structures are unsclerotized and thus similar in form to the *Actia* first instars described here.]

Posterior abdominal segments of first instar ventrally: Segment 7 bare or with tiny spinules posteriorly. Segment 8 with several rows of minute to small spinules anteriorly; one to several rows of tiny to distinct spinules posteriorly. Segment 9 with row or group of tiny to distinct spinules posteriorly; anus small or indistinct.

Examined first instar of: *A. diffidens* (*cf.* Prebble 1935, figs. 4, 5, 30), *A. interrupta, A. lamia, A. malaisei, A.* sp. nr. *parviseta*, New World spp. 4-5 and Zaire sp. 1.

Taxonomic changes

Synonymy of Actia brevis Malloch with Actia darwini Malloch

The male holotypes of these nominal species were examined and compared. They differ primarily in abdominal coloration and setulation of vein CuA_1, but these characteristics vary within some species and the degree of difference present here is not unusual among conspecifics. I also examined other specimens from several localities in eastern Australia, and these exhibit states intermediate between those in the *A. brevis* and *A. darwini* types. I conclude that these types belong to the same species, and here synonymize *Actia brevis* Malloch (1930a) with *Actia darwini* Malloch (1929b).

Actia parviseta Malloch (Fig. 10)

Malloch described this species in 1930 and placed it in his widely defined *Actia*. Later Crosskey (1966: 109) shifted it to *Ceromya*, presumably because it lacks a row of hairs on the katepisternum anterior to the mid coxa - a characteristic usually diagnostic for *Actia*. Dissection of the male genitalia of the type revealed that they possess two *Actia* synapomorphies: a V-shaped S_5 and spinose pregonite. Furthermore, the female reproductive system of a specimen of a closely related species (*A.* nr. *parviseta*) was examined and contained first instars of the *Actia* type (Fig. 171). It thus appears that *Actia parviseta* and few other species (*A. completa, A. magnicornis, A.* nr. *parviseta* and Australia sp. 5) have a bare or sparsely haired katepisternum anterior to the mid coxa, while still possessing all other known synapomorphies of *Actia*.

Hosts

The hosts of *Actia* are better known than those of other siphonines, with records for about 20 *Actia* species (Table 2). Hosts belong predominantly to the Tortricidae, but a variety of other Microlepidoptera and a number of Macrolepidoptera are also parasitized. Host larvae vary in habit from small leaf miners and rollers to large, bare to hairy caterpillars which feed openly on vegetation. There is one record of an *Actia* species parasitic on a pyrrhocorid bug, *Dysdercus* sp. This record is doubtful, as Hemiptera are almost exclusively parasitized by phasiines among the Tachinidae.

Phylogenetics

A row of hairs on the katepisternum anterior to the mid coxa has long been considered a diagnostic feature of *Actia*. It is now apparent that several species belonging to the *Actia* lineage lack this row of hairs (see Recognition and Description sections). The relationships of these species to other *Actia* species is unknown, so the absence of a row of katepisternal hairs from these species cannot be positively polarized as primitive or derived. If derived, then these species must be descended from ancestors possessing a row of katepisternal hairs, and I consider this explanation the more reasonable at this time. This explanation is hypothesized because no other character states support the primitive position of these species within *Actia*, and several of these species have a variable number of katepisternal hairs, ranging from few to a nearly complete row. Thus a row of hairs on the katepisternum is here considered a synapotypy of *Actia* species, with absence of this row in several *Actia* species interpreted as resulting from reversal(s) from the apotypic state.

Almost all *Actia* species have two setulae on the upper portion of the anepisternum (Fig. 31). Most other siphonines have one (Fig. 32), though two are present in few species of *Peribaea* and few species of most supraspecific taxa of *Siphona s.l.* (Table 1). This distribution suggests that two anepisternal setulae is the derived state within the tribe, though its many independent acquistions weaken its value as a synapotypy of *Actia*.

Several species of *Actia* have the anal vein extended to the wing margin (see Recognition and Description sections), but possess the derived genitalic states of *Actia*, and all but one of these (*A. completa*) have a katepisternal row of hairs. Extension of the anal vein to the wing margin probably arose independently in *Actia* and the *Peribaea-Siphona s.l.* lineage.

Sternum 5 is approximately V-shaped in most *Actia* species, and derivable from that shape in the others. The pregonite is J-shaped and spinose, and these states appear to be universal among *Actia* species. It is hypothesized that these characteristics of the male sternum 5 and pregonite are synapotypies of *Actia* (the spinose pregonite proposed as an *Actia* synapotypy by Andersen 1983), and in combination are better diagnostic features of the genus than the row of katepisternal hairs discussed above and previously used to define the genus.

Study of first instars of eight *Actia* species revealed that none has a dorsal cornu on the cephalopharyngeal skeleton (Figs. 168-171). This striking departure from the typical siphonine condition is a synapotypy of *Actia* or a derived subgroup of *Actia*. Farinet's (1980) description and illustration of *A. dubitata* seem to indicate that this species has a dorsal cornu, which if correct supports the latter interpretation. For now I hypothesize that lack of a dorsal cornu in the first instars of the eight *Actia* species studied by me is a synapotypy of the genus, though tentatively pending further investigation.

Previous placement of *Entomophaga exoleta* in *Actia* is discussed in the Phylogenetics section of *Entomophaga* Lioy.

Geographic distribution

Compared to 56 described species in the Old World, the *Actia* fauna of the New World (four described species in the Nearctic region and one in the Neotropical region) at first seems but a minor component of the world fauna. However, this paucity of described *Actia* species gives a false impression of the true diversity of this genus in the New World. I have examined specimens of several new Nearctic *Actia* species, and from relatively meagre collections of Neotropical *Actia*, have recognized close to 20 undescribed species.

The *Actia* fauna of the Old World is much better known than its New World counterpart, though undescribed species undoubtedly live in all regions, particularly the Australian. Distributions are listed in Crosskey (1973, 1976a, 1980) for species of Australia and the Oriental and Afrotropical regions, respectively. There are no adequate keys to aid in the identification of the numerous species of these three regions except for Dear and Crosskey's (1982) key to Philippine species. Malloch's (1930b) key to the Oriental species is long outdated and Mesnil's (1954) key to *Actia* (as *Entomophaga*) species of the upper Congo area only includes about half of the described Afrotropical species.

Palearctic *Actia* are the best studied: most European species can be identified using Mesnil's keys (1963a, 1975: 1399), though species described later by Shima (1970c) and Richter (1974, 1976a, 1980) from Japan and central Asia must be identified from descriptions. Known distributions of several Palearctic *Actia* species have been extended beyond Europe to Israel by Kugler (1979) and to central Asia by Herting (1968b, 1973), Richter (1971, 1975, 1976a,b, 1980, 1981) and Richter and Khitsova (1982). The ranges of all 13 Palearctic species are summarized in Herting (1984) and Norwegian *Actia* are listed in Rognes (1986).

List of described species included in Actia

A *antiqua* (Mesnil), 1954: 31 (*Entomophaga*). Holotype male, Zaire: Bambesa (MRAC). Holotype examined.

N *autumnalis* (Townsend), 1917: 122 (*Actiopsis*). Holotype female, USA: Maryland, Grove Hill (USNM). Holotype examined.

O *brunnea* Malloch, 1930b: 136. Holotype female, Malaysia: Malaya, Kedah Peak (BMNH). Holotype examined.

A *chrysocera* Bezzi, 1923a: 96. Holotype male, Seychelles: Long Island (BMNH). Holotype examined.

A *ciligera* (Mesnil), 1954: 29 (*Entomophaga*). Holotype female, Zaire: L. Kivu (MRAC). Holotype examined.

O *completa* Malloch, 1930b: 139. Holotype male, Malaysia: Malaya, Selangor (BMNH).

Holotype examined.

P *crassicornis* (Meigen), 1824: 351 (*Tachina*). Holotype male, no locality data (MNHN).

syn. *bicolor* (Macquart), 1834: 312 (*Thryptocera*). Type, France: Lille (lost).— Herting, 1976: 3.

claripennis (Robineau-Desvoidy), 1863: 716 (*Thryptocera*). Holotype female, France (MNHN).— Herting, 1974: 19.

flavipalpis (Macquart), 1848: 135 (*Thryptocera*). Holotype female, Switzerland: near Zurich (ETH).— Herting, 1976: 5.

nigripalpis (Robineau-Desvoidy), 1851: 182 (*Thryptocera*). Holotype female (not male), France (MNHN).— Herting, 1974: 19.

palpalis (Rondani), 1859: 14 (*Thryptocera*). Lectotype female (by designation of Herting, 1969a: 198), Italy: Parma (MZF).— Herting, 1969a: 198.

scutellaris (Rondani), 1865: 195 (*Thryptocera*). Holotype male, Italy: Parma (MZF).— Herting, 1969a: 200.

A *cuthbertsoni* Curran, 1933c: 162. Holotype male, Zimbabwe: Gatooma (AMNH).

syn. *cuthbersoni*. Misspelled reference to *cuthbertsoni* Curran (Mesnil, 1977a: 83).

U *darwini* Malloch, 1929b: 334. Holotype male, Australia: Northern Territory, Darwin (SPHTM). Holotype examined.

syn. *brevis* Malloch, 1930a: 309. Holotype male, Australia: New South Wales, Sydney (SPHTM). Holotype examined. New synonymy.

O *deferens* Malloch, 1930b: 130. Holotype female (head lost), Malaysia: Malaya, Kedah Peak (BMNH). Holotype examined.

N *diffidens* Curran, 1933a: 5. Holotype male, Canada: Nova Scotia, Kentville (CNC). Holotype examined.

P *dubitata* Herting, 1971: 12. Holotype female, Switzerland: Delémont (SMNS; not located, maybe lost). Paratype examined.

U *eucosmae* Bezzi, 1926: 239. Holotype female, Australia: Queensland, Milton Farm (published as "Brisbane") (BMNH). Holotype examined.

A *exsecta* Villeneuve, 1936: 416. Two male syntypes, Uganda: Kampala (1 in BMNH). Syntype examined.

A *fallax* (Mesnil), 1954: 29 (*Entomophaga*). Holotype female, Zaire: near Rweru (MRAC). Holotype examined.

O *fulvicauda* Malloch, 1935: 680. Holotype male, Malaysia: Malaya, Selangor (BMNH). Holotype examined.

A *gratiosa* (Mesnil), 1954: 34 (*Entomophaga*). Holotype male, Zaire: L. Kivu (MRAC). Holotype examined.

A *hargreavesi* Curran, 1933c: 160. Holotype female (head missing), Uganda: Kampala (BMNH). Holotype examined.

syn. *comitata* Villeneuve, 1936: 416. Four male and 2 female syntypes, Uganda: Kampala (BMNH).— Crosskey, 1980: 852. Syntypes examined.

P *infantula* (Zetterstedt), 1844: 1047 (*Tachina*). Six syntypes, Sweden: Skåne (UZI).

syn. *antennalis* (Rondani), 1859: 16 (*Thryptocera*). Four syntypes, Italy: Appennines (MZF).— Herting, 1969a: 190.

aristalis (Rondani), 1865: 194 (*Thryptocera*). Two syntypes, Italy: Appennines (MZF).— Herting, 1969a: 190.

villeneuvei. Misspelled reference to *villeneuvii* Strobl (Mesnil, 1963a: 817).

villeneuvii (Strobl *in* Czerny and Strobl), 1909: 221 (*Thryptocera* (*Actia*)). Syntypes, Spain: Elche (NMBA).— Mesnil, 1963a: 817.

N *interrupta* Curran, 1933a: 6. Holotype male, USA: New York, Tuxedo (AMNH). Holotype examined.

P *jocularis* Mesnil, 1957: 47. Holotype male, Japan: Tokura (CNC). Holotype examined.

P *lamia* (Meigen), 1838: 254 (*Roeselia*). Neotype male (by designation of O'Hara, 1985: 95), France: Saint-Sauveur (MNHN). Neotype examined.

syn. *frontalis* (Macquart), 1845: 289 (*Thryptocera*). Replacement name for *A. pilipennis* Robineau-Desvoidy, 1830 (objective synonym).

lamina. Misspelled reference to *lamia* Meigen (Schiner, 1862: 518).

obscurella Robineau-Desvoidy, 1851: 187. Syntypes, France (MNHN).—Herting, 1974: 19.

pilipennis Robineau-Desvoidy, 1830: 86 (junior homonym of *A. pilipennis* (Fallén); replaced by *A. lamia* (Meigen) under Article 60 of the I.C.Z.N.). Lectotype male (by designation of O'Hara, 1985: 95), France: Saint-Sauveur (MNHN). Lectotype examined.

vitripennis Rondani, 1859: 19. Replacement name for *A. pilipennis* Robineau-Desvoidy, 1830 (objective synonym).

U *lata* Malloch, 1930a: 307. Holotype male, Australia: New South Wales, Sydney (SPHTM). Holotype examined.

A *linguata* Mesnil, 1968: 10. Holotype male, South Africa: Cape Town (BMNH). Holotype examined.

A *longilingua* (Mesnil), 1954: 36 (*Entomophaga*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined.

O *magnicornis* Malloch, 1930b: 133. Holotype male, Malaysia: Selangor (BMNH). Holotype examined.

P *maksymovi* Mesnil, 1952b: 153. Holotype male, Switzerland: Engadine (not located; a female paratype from same locality is mislabelled as holotype in CNC). Paratype examined.

syn. *maxymovi*. Misspelled reference to *maksymovi* Mesnil (Richter, 1975: 644 and Richter, 1976a: 572).

O *malaisei* (Mesnil), 1953: 110 (*Crocuta* (*Siphona*)). Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

O *mimetica* Malloch, 1930b: 143. Holotype female, Malaysia: Malaya, Kedah Peak (BMNH). Holotype examined.

P *mongolica* Richter, 1976a: 572. Holotype male, Mongolia: Eastern aimak (ZIL). Holotype examined.

A *munroi* Curran, 1927a: 322. Holotype female, South Africa: Barberton (PPRI).

Holotype examined.

P *nigra* Shima, 1970c: 184. Holotype male, Japan: Hokkaido, Mt. Satsunai, Pirikapetanu (BLKU). Paratype examined.

A *nigrapex* Mesnil, 1977a: 83. Holotype male, Madagascar: Amber Mtn. (MNHN).

O *nigriventris* Malloch, 1935: 680 (as variation of *Actia eucosmae* Bezzi). Holotype female (abdomen lost), Malaysia: Malaya, Selangor (BMNH). Holotype examined.

P *nigroscutellata* Lundbeck, 1927: 462. Two male and 2 female syntypes, Denmark: Tisvilde (ZMUC). Syntypes examined.

A *nitidella* Villeneuve, 1936: 417. Holotype female, Uganda: Kampala (BMNH). Holotype examined.

S *nitidiventris* Curran, 1933a: 4. Holotype female, Panama: Barro Colorado Is. (AMNH). Holotype examined.

P *nudibasis* Stein, 1924: 135. Four syntypes, German Democratic Republic: Crimmitschau (ZMHU).

syn. ? *resinellae* (Schrank), 1781: 478 (*Musca*). Type(s); Austria (lost).— Mesnil, 1963a: 825.

O *oblimata* Mesnil, 1957: 45. Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

U *painei* Crosskey, 1962: 173. Holotype male, New Britain: Rabaul (BMNH). Holotype examined.

A *pallens* Curran, 1927a: 322. Holotype female, South Africa: Natal, Durban (PPRI). Holotype examined.

P *pamirica* Richter, 1974: 1268. Holotype male, USSR: Pamir, Debastia (ZIL). Holotype examined.

U *parviseta* Malloch, 1930a: 308. Holotype male, Australia: New South Wales, Sydney (SPHTM). Holotype examined.

O *pellex* (Mesnil), 1953: 111 (*Crocuta* (*Siphona*)). Holotype female, Burma: Kambaiti (ZMU). Holotype examined.

O *perdita* Malloch, 1930c: 333. Holotype male (head lost), Malaysia: Malaya, Selangor (BMNH). Holotype examined.

O *philippinensis* Malloch, 1930b: 134. Holotype female (head and abdomen lost), Philippines: Luzon, Benguet (USNM). Holotype examined.

A *picipalpis* (Mesnil), 1954: 33 (*Entomophaga*). Holotype female (not male), Zaire: Rutshuru (MRAC). Holotype examined.

P *pilipennis* (Fallén), 1810: 273 (*Tachina*). Lectotype male (by designation of Crosskey, 1974: 302), Sweden (NRS).

syn. *bigoti* (Millière), 1864: 385 (*Morinia*). Type(s), France (lost).— Herting, 1984: 123.

broteas (Walker), 1849: 763 (*Tachina*). Holotype male, England (BMNH).— Crosskey, 1974: 277. Holotype examined.

exscensa (Walker), 1853: 66 (*Tachina*). Holotype female, England (BMNH).— Crosskey, 1974: 283. Holotype examined.

flavisquamis (Robineau-Desvoidy), 1851: 181 (*Thryptocera*). Syntypes, France (MNHN).— Herting, 1974: 19.

humeralis (Robineau-Desvoidy), 1851: 183 (*Thryptocera*). Holotype female, France (lost).— Herting, 1984: 123.

nigrifrons (Robineau-Desvoidy), 1863: 714 (*Thryptocera*). Holotype male, France (MNHN).— Herting, 1974: 19.

reducta Villeneuve, 1920: 66 (as variation of *A. pilipennis* (Fallén), though Villeneuve's description of *A. pilipennis* actually refers to *A. nudibasis* (Herting, *in litt.*)). Type(s), no locality given (not located).

O *pokharana* Shima, 1970b: 275. Holotype male, Nepal: Pokhara (BPBM).

U *pulex* Baranov, 1938: 410. Lectotype male (by designation of Sabrosky and Crosskey, 1969: 35), Solomon Islands: Tulagi (BMNH). Lectotype examined.

U *quadriseta* Malloch, 1936: 20. Holotype female, Australia: New South Wales, Nyngan (SPHTM). Holotype examined.

A *rejecta* Bezzi *in* Bezzi and Lamb, 1926: 569. Holotype male (not female), Rodriguez Is. (BMNH). Holotype examined.

A *rubiginosa* (Mesnil), 1954: 35 (*Entomophaga*). Holotype male, Zaire: Mokoto (MRAC). Holotype examined.

N *rufescens* (Greene), 1934: 34 (*Actiopsis*). Holotype female, USA: South Dakota (USNM). Holotype examined.

A *russula* Mesnil, 1977a: 84. Holotype male, Madagascar: Joffreville (MNHN).

O *siphonosoma* Malloch, 1930b: 136. Holotype male, Malaysia: Malaya, Selangor (BMNH). Holotype examined.

O *takanoi* Baranov, 1935: 557. Lectotype female (by designation of Sabrosky and Crosskey, 1969: 35), Philippines: Luzon, Los Baños (USNM). Lectotype examined.

P *tarsata* Richter, 1980: 541. Holotype female, USSR: Chitinskaya Oblast, Adrianovka (ZIL). Holotype examined.

A *triseta* (Mesnil), 1954: 32 (*Entomophaga*). Holotype male, Rwanda: near Rweru (MRAC). Holotype examined.

A *vulpina* (Mesnil), 1954: 34 (*Entomophaga*). Holotype male, Zaire: Bambesa (MRAC). ? Holotype examined.

O *yasumatsui* Shima, 1970b: 273. Holotype male, Hong Kong: Kowloon, Taipokau (BPBM).

Nomen dubium

P *rubrifrons* (Robineau-Desvoidy), 1830: 87 (*Ceromya*). Type(s), France (lost).— see Herting, 1974: 18.

Nomina nuda

N *labellata* Kamran, 1980: 52.

N *pauciseta* Kamran, 1980: 52.

4.13 Peribaea Robineau-Desvoidy

Figs. 11-12, 27, 60-61, 87-88, 120-121, 139, 153-156, 172-175.

Herbstia Robineau-Desvoidy, 1851: 184 (junior homonym, preoccupied by Edwards, 1834). Type-species, *H. tibialis* Robineau-Desvoidy, 1851 (monotypy).

Peribaea Robineau-Desvoidy, 1863: 720. Type-species, *P. apicalis* Robineau-Desvoidy, 1863 (by designation of Coquillett, 1910: 587).

Strobliomyia Townsend, 1926c: 31. Type-species, *Thryptocera fissicornis* Strobl, 1910 (original designation).

Eogymnophthalma Townsend, 1926a: 35. Type-species, *E. orientalis* Townsend, 1926 (original designation) = *Tachina orbata* Wiedemann, 1830.

Talaractia Malloch, 1930a: 305 (as subgenus of *Actia*). Type-species, *Actia* (*Talaractia*) *baldwini* Malloch, 1930 (original designation).

Tararactia. Mispelled reference to *Talaractia* Malloch (Malloch, 1930a: 305).

Uschizactia Townsend, 1934: 248. Type-species, *Actia uniseta* Malloch, 1930 (original designation).

Recognition

Species of the genus *Peribaea* are widely distributed throughout the Old World, and are easily recognized among siphonines by their possession of a strong, downwardly directed, proepimeral seta (Fig. 27). Species of *Chaetostigmoptera* Townsend and the Neaerini, and several other tachinids, also have a distinctly developed, downwardly directed, proepimeral seta (varied from weak to strong), though other differences indicate that this similarity is due to convergence. Together, *Peribaea* and *Siphona s.l.* are distinguishable from other siphonines (and almost all other tachinids) by having the anal vein extended to the wing margin.

Description

Length: 2.5-5.0mm.

Head (Figs. 11-12).— Five frontal setae, normal arrangement. Anterior proclinate orbital seta longer than posterior one in most species. Eye of male and female subequal in size, medium to large, 0.73-0.86 head height; size in female subequal to that of male. Flagellomere 1 of male markedly varied in length, 0.39-0.75 head height; shape from linear or broad to bifid (*e.g.* figs. 3a, 4a and 5a in Shima 1970a), trifid (*P. jepsoni* and *P. trifurcata*; *e.g.* fig. 2a, *op. cit.*), or pectinate (*P. baldwini*, *P. cervina* and *P. pectinata*; Fig. 11 and fig. 1a, *op. cit.*). Flagellomere 1 of female simple, not bifid. Aristomere 1 short. Aristomere two 1.5-12X longer than wide (2-4X in most species). Aristomere 3 long and evenly tapered in most species, short and thickened to near tip in few; almost bare to short plumose, in most species micropubescent. Clypeus U-shaped in most species, only slightly broadened in few. Palpus short, clavate. Proboscis with prementum short to medium (not elongate), labella padlike.

Thorax (Fig. 27).— Prosternum setulose. Lower proepimeral seta strong and directed downward (Fig. 27). Katepisternum bare anterior to mid coxa. Lower katepisternal seta slightly shorter than or subequal in length to upper anterior seta in most species, slightly longer in very few. Four postsutural dorsocentral setae (apparently never three). Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Tarsomeres normal in size, or tarsomere 5 of fore leg elongate and broadened (only known in female of *P. lobata*); claws short in most species, medium in very few. Wing: CuA_1 with distal portion 0.63-1.3X length of proximal portion (mean 0.84); anal vein extended to wing margin. Wing setulae: R_1 dorsally bare, or distally or entirely setulose, ventrally bare or distally setulose; R_{2+3} bare except setulose dorsally and ventrally in *P. modesta*; R_{4+5} setulose from base to beyond *r-m*; CuA_1 bare in almost all species (few sparsely setulose).

Abdominal terga 1-5.— Abdomen ovoid in most species, markedly elongate in few, and very elongate in *P. ugandana*. T_{1+2} without median marginal setae; lateral marginal setae absent from most species, strong in few. T_3-T_5 average in most species, with extra pair of lateral marginal setae on T_3 in few, weak lateral discal setae on T_4-T_5 in *P. discicornis*.

Male genitalia (Figs. 60-61, 87-88, 120-121, 139).— S_5 markedly varied, inner (or posterior) margins of processes obtusely angled (Fig. 60) to almost transverse in most species, in very few species V-shaped (Fig. 61; resembling typical *Actia* shape except median cleft more distinct); apical lobe undifferentiated to slightly differentiated; median lobe slightly to broadly rounded in most species, rather elongate and/or flattened medially or posteromedially in few; processes moderately setulose, with three to six pair of large setae in most species. T_6 varied from small pair of lateral sclerites to single, broad, dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion wider than hypandrial apodeme in most species, subequal in width in very few; some species with weak ring-like sclerotized sheath basally (*e.g. P. apicalis*). Pregonite (Figs. 87-88) in profile approximately C-shaped, broad at mid length; bare. Epiphallus present or absent, where present generally narrow. Distiphallus (Figs. 120-121) large, posterior margin complete, variously incised laterally, distinctly broader than long in ventral view. Postgonite apically rounded, pointed, or turned outward. Surstylus (Fig. 139) average length to long, broad in few species, straight to curved posteriorly; basally free from epandrium in most species (Fig. 139), fused with epandrium in few (*e.g. P. trifurcata*); apically enlarged in some species, greatly swollen in few, in one (?undescribed) species from Australia subapically with small medially-directed lobe. Cerci short in most species (Fig. 139), average length in few, in profile straight along posterior margin or smoothly curved at midlength; moderately setose on basal half.

Examined male genitalia of: ***P. apicalis, P. fissicornis, P. repanda, P. ?similata, P. tibialis, P. ugandana***, Africa spp. 1-4, Australia spp. 1-3, Nepal sp. 1 and Sri Lanka sp. 1. Examined published figures of: ***P. fissicornis*** (Andersen 1983, fig. 18), ***P. hirsuta, P. illugiana, P. pectinata, P. sedlaceki, P. trifurcata*** (all five in Shima 1970a, figs. 1-5), ***P. insularis*** (Shima 1970c, figs. 1, 3a), ***P. alternata*** and ***P. aegyptia*** (both in Shima 1981, figs. 1 and 3, the latter species as ***P. orbata***).

Female genitalia (Figs. 153-156).— Varied from short and unmodified (Fig. 153) to extremely elongate (Figs. 155-156). S_6 bare or with very short hairs; in primitive forms S_6

and S_7 flat and wider than long, in derived forms both sterna slightly to sharply keeled medially and pointed posteriorly in most species, in very specialized forms both sterna elongate and tip of S_7 extended over cerci, with intersegmental membrane similarly elongate (Figs. 155-156); S_7 without anterior apodeme. T_6 distinctly developed and enclosing spiracles of segment 6; dorsally continuous or discontinuous. T_7 present as lateral sclerites in unmodified forms, fused with S_7 in some derived forms with S_7 elongate (Figs. 154-156); enclosing spiracles of segment 7. S_8 bare, absent (particularly in elongate forms) to average-sized, flat sclerite. T_{10} absent from some species, present as a small to medium median sclerite in others.

Examined female genitalia of: ***P. fissicornis***, ***P. tibialis***, ***P. ugandana***, Africa spp. 2-5 and Australia spp. 1,3. Examined published figures of: ***P. alternata***, ***P. aegyptia*** (both in Shima 1981, fig. 2, the latter as ***P. orbata***) and ***P. tibialis*** (Andersen 1983, fig. 4).

First instar (Figs. 172-175).— Cephalopharyngeal skeleton: Labrum narrow to hook-like in most species, dorsoventrally parallel-sided and anteriorly bluntly rounded in Africa sp. 5 (Fig. 175). Lateral sclerite unmodified or divided into two sclerites. Hypopharyngeal sclerite unmodified. Both dorsal and ventral cornua present; ventral cornu relatively large in some species (especially Africa sp. 3, Fig. 173).

Posterior abdominal segments of first instar ventrally: Segment 7 bare or almost so posteriorly. Segment 8 with as many as several sparse rows of tiny spinules anteriorly; two or three uneven rows of uniform-sized spinules posteriorly. Segment 9 bare posteriorly; anus average-sized.

Examined first instar of: ***P. tibialis*** (*cf.* figs. 32-33 in Farinets 1980 and fig. 26 in Andersen 1983), ***P. ugandana***, Africa spp. 3-5 and Australia spp. 1, 3.

Taxonomic changes

Identity of Tachina orbata Wiedemann

The type of ***Tachina orbata*** Wiedemann (1830: 336) is lost. In 1967 Crosskey designated a neotype for this species, believing ***T. orbata*** to be a widespread Old World species of ***Peribaea***. According to Mesnil (***in litt.***), the original description of ***T. orbata*** clearly refers to a neaerine, and *P. aegyptia* (Villeneuve) is the valid name for the species Crosskey thought was Wiedemann's *T. orbata*. Crosskey's neotype designation is invalid, and the matter will be discussed by Shima in a forthcoming paper (*in litt.*).

Status of Peribaea subaequalis (Malloch)

Malloch described *P. monticola, P. rotundipennis* and *P. subaequalis* from specimens collected in the Cuernos Mts. on Negros Island in the Philippines. The first two names were synonymized with *P. orbata* (now *P. aegyptia*) by Crosskey (1966: 107), while the third has continued to be cited as valid (Crosskey, 1976: 214). I examined all three of Malloch's types along with specimens of *P. aegyptia*, and found no substantial difference among them. Unfortunately, Malloch's type specimens are not ideal for comparison because all three lack heads, and two are females while the third is a male. Nevertheless, the fact that Malloch's types were collected from the same locality (dates unknown) and are similar to one another and to specimens of *P. aegyptia* in such important characteristics as wing vein setulation and abdominal coloration strongly suggests that they are all conspecific. (Even Malloch stated that his specimens "may ultimately prove to be mere variations within a single species" (1930b: 142).) The one difference, anal vein not extended to wing margin in the type of *P. subaequalis*, is very rare in *Peribaea* and not typical of any known species, so probably represents an aberration in this specimen (even the paratypes of *P. subaequalis* have the anal vein reaching wing margin). For all these reasons I feel confident in adding *P. subaequalis* to the list of synonyms of the widespread species *P. aegyptia*.

Hosts

Hosts of *Peribaea* species belong to several families of Microlepidoptera and Macrolepidoptera (Table 2). The most commonly parasitized group is the Noctuoidea, accounting for half the total records.

Adult females of *Peribaea* species are thought to larviposit directly on their hosts (Herting 1957). Presumably the elongate ovipositor of some *Peribaea* species is an adaptation to this behavior.

Phylogenetics

The monophyly of *Peribaea* is well established (Andersen 1983: 10). Adults possess externally a strong, downwardly directed, proepimeral seta (Fig. 27). This state is unique to *Peribaea* among siphonines, though is convergently, and often more weakly, developed in species of *Chaetostigmoptera* Townsend and the Neaerini, and several other tachinids. The distiphallus is varied in shape among *Peribaea* species, though its sclerotized posterior surface is a shared characteristic and is hypothesized as a synapotypy; the partially unsclerotized posterior surface in all but very few other (unrelated) siphonines (see Table 1) is interpreted as plesiotypic. Sternum 8 in the female genitalia is bare in all examined *Peribaea* species, though several derived species lack this sclerite entirely (Figs. 154-156). A bare, unsclerotized sternum 8 is considered synapotypic of the genus, and absence of sternum 8 is interpreted as a more derived condition (sternum 8 convergently lost in few other siphonines; see Table 1).

The labrum of first instars of *Peribaea* species is apically narrowed or hook-like (Figs. 172-175), in contrast to the hatchet-like labrum of most other siphonines. More primitive siphonine lineages have the latter condition (with the known exception of *Ceromya silacea*, Fig. 160), so the former state is presumed to be derived in *Peribaea*. No evidence suggests that the hook-like labrum of most *S. (Pseudosiphona)* species (Figs. 188-193) is not independently derived, as the labrum is hatchet-like in other *Siphona s.l.* taxa (Figs. 176-209) and *S. (Pseudosiphona)* is probably not the most primitive lineage of that genus (see Evolution chapter).

Geographic distribution

Forty-five described species are recognized in *Peribaea*, and all are restricted to the Old World. Greatest diversity, accounting for almost half the described species, is recorded from the Afrotropical region (particularly the upper Congo area, as a result of Mesnil's work on the siphonines of that area; distributions in Crosskey 1980). More modest diversity is found in the three other Old World regions. Oriental species are listed in Crosskey (1976a; Philippine species keyed in Dear and Crosskey 1982) and Australian species in Crosskey

(1973) and Shima (1970a, with key to Papuan species; 1981). Most Palearctic *Peribaea* species are redescribed and keyed in Mesnil (1963a; also key to separate *P. apicalis* and *P. tibialis* in Herting 1968a). Other records for Palearctic species are given in Mesnil and Pschorn-Walcher (1968), Herting (1968b, 1969b), Crosskey (1976b), Kugler (1979) and Richter (1971, 1975, 1976a, 1980, 1981), Rognes (1986), and summarized in Herting (1984).

I suspect that the preponderance of described species in the Afrotropical region accurately reflects the true pattern of *Peribaea* diversity. Presence of ten species in the Australian region (including one on the Solomon Islands), seven species on Madagascar (Mesnil 1977a) and one each on Mauritius and Seychelles Islands, indicates that the dispersal power of some members of this genus are as great as in other siphonine genera that are distributed worldwide. It is therefore puzzling that *Peribaea* has not reached the New World. Hosts do not seem to be the limiting factor, as many host genera are Holarctic or cosmopolitan in distribution.

List of described species included in Peribaea

O,P,A,U ***aegyptia*** (Villeneuve), 1912: 508 (*Gymnopareia* (*Actia*)). Lectotype male (by designation of Crosskey, 1966: 108), Egypt: Qaliub (BMNH). Lectotype examined.

syn. ***monticola*** (Malloch), 1930b: 143 (*Actia*). Holotype male (head lost), Philippines: Negros, Cuernos Mtns. (USNM).— Crosskey, 1966: 107. Holotype examined.

nigripes (Curran), 1927c: 6 (*Actia*). Holotype male, Zaire: Boma (AMNH).— Crosskey, 1980: 853. Holotype examined.

nigritula (Malloch), 1930a: 309 (*Actia*). Holotype female, Australia: Queensland, Cairns (SPHTM).— Crosskey, 1966: 107. Holotype examined.

orientalis (Townsend), 1926a: 35 (*Eogymnophthalma*). Lectotype male (by fixation of Townsend, 1940: 213), Indonesia: Sumatra, Fort de Kock (ZMA).— Crosskey, 1966: 107. Lectotype examined.

rotundipennis (Malloch), 1930b: 143 (*Actia*). Holotype female (head lost), Philippines: Negros, Cuernos Mtns. (USNM).— Crosskey, 1966: 107. Holotype examined.

sororcula (Mesnil), 1954: 16 (*Strobliomyia*). Holotype female, Zaire: Rutshuru (MRAC).— Crosskey, 1976a: 214. Holotype examined.

subaequalis (Malloch), 1930b: 142 (*Actia*). Holotype male (head lost), Philippines: Negros, Cuernos Mtns. (USNM). Holotype examined. New synonymy.

U *alternata* Shima, 1981: 445. Holotype male, New Guinea: Wau, Mt. Kaindi (BPBM). Paratype examined.

A *annulata* (Mesnil), 1954: 21 (*Strobliomyia*). Holotype male, Zaire: Rwankwi (MRAC). Holotype examined.

A *anthracina* Mesnil, 1977a: 81. Holotype male, Madagascar: Belazao (MNHN).

P *apicalis* Robineau-Desvoidy, 1863: 721. Holotype male (head and abdomen lost), France: Saint Sauveur (MNHN).

U *argentifrons* (Malloch), 1930a: 309 (*Actia*). Holotype male, Australia: New South Wales, Sydney (SPHTM). Holotype examined.

syn. *angustifrons*. Mispelled reference to *argentifrons* Malloch (Hardy, 1959: 213).

U *baldwini* (Malloch), 1930a: 306 (*Actia* (*Talaractia*)). Holotype male, Australia: Queensland, Palm Is. (SPHTM). Holotype examined.

A *cervina* (Mesnil), 1954: 18 (*Strobliomyia*). Holotype male, Zaire: Rutshuru (IRSN). Holotype examined.

A *clara* (Mesnil), 1954: 21 (*Strobliomyia*). Holotype male, Zaire: Katanga, Kalabi (MRAC). Holotype examined.

A *compacta* (Curran), 1927a: 324 (*Actia*). Holotype male (head lost), South Africa: East London (PPRI). Holotype examined.

P *discicornis* (Pandellé), 1894: 109 (*Thryptocera*). Holotype male, France: Pyrenees, Tarbes (IRSN).

A *ferina* (Mesnil), 1954: 17 (*Strobliomyia*). Holotype male, Rwanda: Kibga (MRAC). Holotype examined.

P *fissicornis* (Strobl), 1910: 139 (*Thryptocera*). Holotype male (not female), Austria: "Styria" (NMBA).

A *gibbicornis* (Mesnil), 1954: 19 (*Strobliomyia*). Holotype male, Zaire: Rutshuru (IRSN). Holotype examined.

U *hirsuta* (Shima), 1970a: 269 (*Strobliomyia*). Holotype male, New Guinea: Popondetta (BPBM).

O *hyalinata* (Malloch), 1930b: 138 (*Actia*). Holotype female (not male), Malaysia: Malaya, Selangor (BMNH). Holotype examined.

U *illugiana* (Shima), 1970a: 265 (*Strobliomyia*). Holotype male, New Britain: Gazelle Penn., Illugi (BPBM).

O *insularia* (Shima), 1970c: 179 (*Strobliomyia*). Holotype male, Japan: Ryukyu Islands, Amami Is., Tokunoshima (BLKU).

A *jepsoni* (Villeneuve), 1937: 2 (*Strobliomyia*). Holotype male, Mauritius (CNC). Holotype examined.

P *leucopheae* (Mesnil), 1963b: 33 (*Strobliomyia*). Holotype female, USSR: Tadjikistan, Varzoba (ZIL). Holotype examined.

A *lobata* Mesnil, 1977a: 80. Holotype male, Madagascar: Manjakatatompo (MNHN).

A *longiseta* (Villeneuve), 1936: 417 (*Actia*). Holotype female, Uganda: Kampala (BMNH). Holotype examined.

O *malayana* (Malloch), 1935: 678 (*Actia*). Holotype male (abdomen lost), Malaysia: Malaya, Selangor (BMNH). Holotype examined.

A *mitis* (Curran), 1927a: 323 (*Actia*). Syntypes, South Africa: Barberton (PPRI). Syntypes examined.

A *modesta* (Mesnil), 1954: 14 (*Strobliomyia*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined.

• "*orbata*" (Wiedemann), 1830: 336 (*Tachina*). Identity discussed in text under section on *Peribaea*. Neotype examined.

P *palaestina* (Villeneuve), 1934: 57 (*Actia*). Holotype female, Israel: Rehoboth (SMNS).

Holotype examined.

syn. *alipes* (Villeneuve), 1942b: 134 (*Actia*). Holotype female, Egypt: Assuan (CNC).— Herting, 1982: 8. Holotype examined.

U *pectinata* (Shima), 1970a: 261 (*Strobliomyia*). Holotype male, New Britain: Gazelle Penn., Illugi (BPBM).

U *plebeia* (Malloch), 1930a: 310 (*Actia*). Holotype male, Australia: New South Wales, Coramba (SPHTM). Holotype examined.

syn. *plebia*. Mispelled reference to *plebeia* Malloch (Hardy, 1959: 213).

A *pulla* Mesnil, 1977a: 82. Holotype male, Madagascar: Ambato-Boeni (MNHN).

A *repanda* (Mesnil), 1954: 16 (*Strobliomyia*). Holotype male, Zaire: nr. Rwindi, Ndeko (MRAC). Holotype examined.

A *rubea* Mesnil, 1977a: 82. Holotype female, Madagascar: Amber Mtn. (MNHN).

U *sedlaceki* (Shima), 1970a: 267 (*Strobliomyia*). Holotype male, New Guinea: Popondetta (BPBM).

O *setinervis* (Thomson), 1869: 519 (*Thryptocera*). Holotype female, China (NRS).

O,P *similata* (Malloch), 1930b: 137 (*Actia*). Holotype male, Malaysia: Malaya, Selangor (BMNH). Holotype examined.

A *spoliata* (Bezzi), 1923a: 95 (*Actia*). One male and 1 female syntype, Seychelles Islands (BMNH). Syntypes examined.

U *stiglinae* (Bezzi), 1928: 204 (*Actia*). Holotype male (not female), Fiji: Lautoka (BMNH). Holotype examined. **New combination**, moved from *Actia*.

O,A *suspecta* (Malloch), 1924: 409 (*Actia*). Holotype male (not female), India: Bihar, Pusa (BMNH). Holotype examined.

syn. *nana* (Curran), 1928: 237 (*Actia*). Holotype female, Uganda: Kampala (BMNH).— Crosskey, 1976a: 214. Holotype examined.

P,A *tibialis* (Robineau-Desvoidy), 1851: 185 (*Herbstia*). Holotype male, France: Saint Sauveur (lost).

syn. *flavicornis* Robineau-Desvoidy, 1863: 721. Holotype female, France: Lozère

(MNHN).— Herting, 1974: 19.

minuta Robineau-Desvoidy, 1863: 722. Holotype female, France (MNHN).— Herting, 1974: 19.

A *timida* (Mesnil), 1954: 18 (*Strobliomyia*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined.

U *trifurcata* (Shima), 1970a: 263 (*Strobliomyia*). Holotype male, New Guinea: Popondetta (BPBM).

A *ugandana* (Curran), 1933c: 161 (*Actia*). Holotype male, Uganda: Kampala (BMNH). Holotype examined.

O *uniseta* (Malloch), 1930b: 129 (*Actia*). Holotype male (head lost), Malaysia: Malaya, Selangor (BMNH). Holotype examined.

P *ussuriensis* (Mesnil), 1963a: 807 (as subspecies of *Strobliomyia hyalinata* (Malloch)). Holotype male, USSR: Ussuri, Sučan (ZIL). Holotype examined.

A *vidua* (Mesnil), 1954: 15 (*Strobliomyia*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined.

4.14 Siphona Meigen

Figs. 13-20, 22, 24-26, 28, 30, 32, 34, 36, 38, 43-46, 62-70, 89-106, 122-136, 140-144, 176-209.

Recognition

Siphona Meigen, as considered here in the broad sense, is a diverse, monophyletic group of cosmopolitan distribution. Adults are morphologically varied, but all are characterized by the anal vein extended to the wing margin at least as a sharply creased fold (Fig. 22). This state is also shared by *Peribaea* species, but these are easily recognized by their two strong and opposed proepimeral setae (one strong proepimeral seta in *Siphona s.l.* species and other siphonines, *cf.* Figs. 27 and 28).

Three known Old World *Actia* species are easily confused with *Siphona s.l.* species because they have the anal vein extended to the wing margin. They differ from members of

Siphona s.l. in their possession of a partial to complete row of katepisternal hairs and distinctive *Actia*-type male genitalia (see Recognition section of *Actia*).

Though not very useful for general identification purposes, two features of first instars are diagnostic (and synapotypic) of *Siphona s.l.* species; both on the ventral surface of the abdomen on segments 7 and 8. Segment 7 in *Siphona s.l.* species is equipped posteriorly with from two, to a row of about 10, large spinules or hooks (Figs. 176-209). Other siphonines are bare in this region or have tiny spinules (Figs. 157-163, 165-175) with the exception of *Ceromya* Australia sp. 3 (Fig. 164). *S. (Aphantorhaphopsis)* Uganda sp. 1 (Fig. 180) is the only known *Siphona s.l.* species without the typical condition of the genus. The spinulose condition on the ventral surface of segment 8 posteriorly also distinguishes almost all *Siphona s.l.* species from other siphonines. With the exception of few species (see Table 1), *Siphona s.l.* species (Figs. 176-209) have a single dominant row of spinules in this position and other siphonines (Figs. 157-175) have two or more even or uneven rows of spinules.

4.15 Siphona (Actinocrocuta Townsend)

Figs. 13, 62, 89, 122-123, 142, 182.

Actinocrocuta Townsend, 1935: 228. Type-species, *A. chaetosa* Townsend, 1935 (original designation) = *Tachina singularis* Wiedemann, 1830. New status under *Siphona* Meigen.

Recognition

Adults of this Neotropical group of few species cannot be distinguished from all other *Siphona s.l.* species except by features of the male genitalia, though the following external characteristics are shared by the known species: yellow overall except for varied amounts of reddish brown at femoral-tibial articulations, surrounding marginal setae on abdomen, and along abdominal midline; abdomen very sparsely pruinose; lower katepisternal seta at least length of upper anterior seta; three postsutural dorsocentral setae; wing vein R_{4+5} setulose from base to beyond crossvein *r-m*; and anal vein extended to wing margin. The following combination of male genitalic states is unique to *S. (Actinocrocuta)* species: pregonite slender, apically rounded and covered with tiny spinules (Fig. 89; more curved than in Fig. 100); distiphallus in profile slender, nearly parallel-sided, varied apically (Figs. 122-123); and cerci in posterior view broadened to near tip (Fig. 142; more broadened than in some *S. (Aphantorhapha)* species [Fig. 143], though similar in shape in very few other *Siphona s.l.* species).

Description

Length: 3.5-4.5mm.

Head (Fig. 13).— Anterior proclinate orbital seta longer than posterior one. Eye of male and female subequal in size, medium to medium-large, 0.76-0.81 head height. Flagellomere 1 of male and female subequal, medium-short to medium length, 0.41-0.52 head height; average width. Aristomere 1 short. Aristomere 2 relatively short, about 1.5X longer than wide. Aristomere 3 long and evenly tapered, pubescent to short plumose. Clypeus narrow and enclosed in membrane to slightly broadened. Palpus short, clavate. Proboscis with prementum medium in length (slightly over half head height in length), labella padlike to moderately lengthened.

Thorax.— Prosternum setulose. Lower katepisternal seta longer than upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.35-0.49 length of proximal portion (mean 0.42). Wing setulae: *Sc* ventrally setulose in some specimens; R_1 dorsally distally or entirely setulose, ventrally bare; R_{4+5} setulose from base to beyond *r-m*; CuA_1 bare or setulose.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent to weak. T_3-T_5 with average setation.

Male genitalia (Figs. 62, 89, 122-123, 142).— S_5 (Fig. 62) with posterior margins of processes approximately U-shaped; apical lobe distinctly differentiated, apex curved inward in some specimens of *S. singularis* complex; median lobe pointed to narrowly rounded, relatively unmodified; processes moderately setulose. T_6 apparently absent. Ejaculatory apodeme with fan-shaped portion subequal to 2.0X wider than width of hypandrial apodeme. Pregonite (Fig. 89) in profile rather slender and elongate; outer surface short spinose apically, tiny seta posteriorly in *S. singularis* complex, seta absent from single specimen of *S. (A.)* sp. 1. Epiphallus absent. Distiphallus reduced posteriorly, not incised laterally, in profile rather narrow basally, nearly parallel-sided to tip, in *S. singularis* complex with or without (Fig. 122) apical hook anteroventrally, in *S. (A.)* sp. 1 with several hooks radiated from apex ventrally and anteroventrally (Fig. 123). Postgonite rounded apically in *S. singularis* complex, short in *S. (A.)* sp. 1. Surstylus rather short to average length, more or less straight; basally free from epandrium. Cerci average length, in profile rather straight at midlength, in posterior view broadened to near apex (Fig. 142); moderately setose on basal half in *S. (A.)* sp. 1, varied in members of *S. singularis* complex from state in *S. (A.)* sp. 1 to densely setose along length.

Examined male genitalia of: *S. singularis* complex, *S. (A.)* sp. 1.

Female genitalia— Moderately extensible. S_6 bare to sparsely haired posteromedially; slightly keeled posteromedially. T_6 absent; spiracles of segment 6 in membrane dorsal to lateral margins of S_6. S_7 with long anterior apodeme; slightly keeled posteromedially. T_7 absent; (spiracles not located). S_8 much broader than average, haired. T_{10} present as two sclerites.

Examined female genitalia of: *S. singularis*.

First instar (Fig. 182).— Cephalopharyngeal skeleton: Labrum hatchet-like. Lateral sclerite very broad. Hypopharyngeal sclerite unmodified. Both dorsal and ~~ventral cornua~~ present.

Posterior abdominal segments of first instar ventrally: Segment 7 with four large hooks posteriorly. Segment 8 with row of moderate-sized spinules anteriorly; one row of smaller, uniform-sized spinules posteriorly. Segment 9 bare posteriorly; anus average-sized.

Examined first instar of: *S. singularis*.

Taxonomic changes

Synonymy of S. (Actinocrocuta) chaetosa (Townsend) with S. (Actinocrocuta) singularis

(Wiedemann)

The primary types (both male) of *S. chaetosa* (type locality "Trinidad") and *S. singularis* (type locality "Brasilia") are externally very similar, with no significant differences. The male genitalia are less similar, differing particularly in features of the distiphallus and degree of setation on posterior surface of cerci. In the absence of additional material I would be inclined towards retaining both names, but additional material has been examined and includes not only specimens with clearly intermediate states but also specimens with more extreme states. I have not been able to sort these specimens into distinct morphological groups because the apparent differences seem continuous and are not clinally distributed. There is either one very morphologically varied species, or two or more sibling species. Due to the range of observed variation and presence of intermediates, I synonymize the name *S. chaetosa* (Tnsd.) with *S. singularis* (Wied.), and refer to this varied taxon as the *S. singularis* complex.

Hosts. Unknown.

Phylogenetics

Siphona (Actinocrocuta) here comprises the *S. singularis* complex and *S. (Actinocrocuta)* sp. 1. Adults of these taxa are similar in external appearance and coloration (see Recognition section), but these characteristics alone are not good indicators of monophyly because convergence in such features is common among *Siphona s.l.* species. Monophyly of this subgenus is better supported by characters of the male genitalia. *S. (Actinocrocuta)* species share a unique combination of genitalic states, including broadened cerci (Fig. 142), slender distiphallus (Figs. 122-123) and slender and apically spined pregonite (Fig. 89). Though at least the first and last states are individually present in a few other *Siphona s.l.* species, the possession of all three states in *S. (Actinocrocuta)* species is good evidence that the taxon is monophyletic. The sister group to *S. (Actinocrocuta)* cannot be established with confidence (it is certainly to be sought among other Neotropical *Siphona s.l.* taxa), so *S. (Actinocrocuta)* is retained as a narrowly defined subgenus of *Siphona s.l.*

Geographic distribution

The *S. singularis* complex is widely distributed throughout the Neotropics, with records from Costa Rica, Colombia, Ecuador, Peru, Brazil (Manaus and southeastern region) and Trinidad. A single male specimen of a new species, referred to above as *S. (A.)* sp. 1, was collected at 400m from Avispas, Madre de Dios, Peru (1-15.X.1962), along with several specimens of the *S. singularis* complex.

List of described species included in Siphona (Actinocrocuta)

S *singularis* (Wiedemann), 1830: 335 (*Tachina*). Holotype male, Brazil (FSF). Holotype examined.

syn. *chaetosa* (Townsend), 1935: 228 (*Actinocrocuta*). Lectotype male (by designation of Townsend, 1940: 275), Trinidad (USNM). Lectotype examined. **New synonymy.**

4.16 Siphona (Aphantorhapha Townsend)

Figs. 14, 63, 90, 124, 143, 183.

Aphantorhapha Townsend, 1919: 586. Type-species, *A. arizonica* Townsend, 1919 (original designation). **New status** under *Siphona* Meigen.

Recognition

As presently conceived, *S. (Aphantorhapha)* comprises two described and four undescribed New World species, and is one of the more difficult *Siphona* subgenera to diagnose. Adults are rather small (2.0-3.5mm in length) and dark-colored, with more or less average-sized eye and flagellomere 1, three postsutural dorsocentral setae, lower katepisternal seta subequal to or longer than upper anterior seta, crossvein *dm-cu* slightly removed from wing margin, and anal vein extended to wing margin. As these external characteristics are shared by some other species of *Siphona s.l.*, the male genitalia of specimens must be examined for a reliable identification.

One of the two distinctive features of the male genitalia of *S. (Aphantorhapha)* species is the shape of the distiphallus (Fig. 124), which in profile has a characteristically tapered appearance and rounded to pointed tip. The other distinctive feature, though not present in all species (absent from single examined male of *S. atoma* and some specimens of *S. arizonica*), is the slightly broadened cerci (Fig. 143; broadened at midlength rather than to near tip like in *S. (Actinocrocuta)* species, Fig. 142). Like many other *Siphona s.l.* species, the pregonite (Fig. 90) is of average shape, apically bare, and with or without a seta posteriorly.

Description

Length: 2.0-3.5mm.

Head (Fig. 14).— Proclinate orbital setae subequal in length or anterior one longer. Eye of male medium to medium-large, 0.71-0.83 head height; eye of female slightly smaller to slightly larger than in male. Flagellomere 1 of male medium-short to medium length, 0.43-0.54 head height; shape from linear to broadened. Flagellomere 1 of female shorter than in male. Aristomere 1 short. Aristomere two 2.0-4.0X longer than wide. Aristomere 3 long and evenly tapered to short and thickened to near tip, micropubescent to short plumose. Clypeus narrow and enclosed in membrane to slightly broadened. Palpus short, clavate. Proboscis with prementum short to medium in length (about half head height in length), labella padlike in most species, slightly lengthened in *S. (A.)* sp. 2.

Thorax.— Prosternum setulose. Lower katepisternal seta subequal in length or longer than upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.44-0.85 length of proximal portion (mean 0.64). Wing setulae: R_1 dorsally bare or entirely setulose, ventrally bare or distally setulose; R_{4+5} setulose to or beyond *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent to weak. T_3-T_5 with average setation.

Male genitalia (Figs. 63, 90, 124, 143).— S_5 (Fig. 63) with posterior margins of processes slightly obtuse to approximately U-shaped; apical lobe distinctly differentiated, apex curved inward in some species; median lobe rounded to broadly truncate, relatively unmodified; processes moderately setulose. T_6 absent or present as two lateral sclerites or broad dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion subequal to 1.5X wider than width of hypandrial apodeme. Pregonite in profile smoothly curved anteriorly (Fig. 90) to rather sharply bent anteriorly at midlength, and more or less pointed apically; posteriorly bare in single specimen of *S. (A.)* sp. 2, with tiny to medium-sized seta in *S. arizonica*, short seta in single examined specimens of *S. atoma* and *S. (A.)* spp. 3 and 4 and medium-sized seta in single examined specimen of *S. (A.)* sp. 1. Epiphallus absent. Distiphallus reduced posteriorly, not incised to slightly incised laterally, with enlarged teeth anterolaterally in *S. arizonica* (Fig. 124) and to lesser extent *S. atoma*, teeth not enlarged beyond size of adjacent spinules in *S. (A.)* spp. 1 to 4, in profile tapered to rounded or pointed tip. Postgonite apically rounded. Surstylus short to rather long and straight; basally free from epandrium. Cerci in profile short in *S. arizonica* and *S. atoma*, average length in *S. (A.)* spp. 1 to 4; straight to smoothly curved along posterior margin; slightly broadened at midlength in posterior view in some specimens of *S. arizonica* and single dissections of *S. (A.)* spp. 1-4 (Fig. 143), smoothly tapered to tip in some specimens of *S. arizonica* and single dissection of *S. atoma* (similar to Fig. 144); moderately setose on basal half.
Examined male genitalia of: *S. arizonica, S. atoma* and *S. (A.)* spp. 1 and 2.

Female genitalia.— Short. S_6 with average length hairs. T_6 absent or present as median sclerite; spiracles of segment 6 in membrane dorsal to lateral margins of S_6. S_7 with long anterior apodeme; not keeled posteromedially. T_7 absent or present as small lateral sclerites; spiracles of segment 7 in membrane between segments 6 and 7. S_8 distinctly developed, haired. T_{10} present as two sclerites.
Examined female genitalia of: *S. arizonica.*

First instar (Fig. 183).— Cephalopharyngeal skeleton: Labrum hatchet-like; angled slightly downward. Lateral sclerite unmodified. Hypopharyngeal sclerite unmodified. Both dorsal and ventral cornua present.

Posterior abdominal segments of first instar ventrally: Segment 7 with four large spines posteriorly. Segment 8 with several uneven rows of small spinules anteriorly; one row of spinules posteriorly, comprised of about five large spinules medially and small spinules laterally. Segment 9 bare posteriorly; anus average-sized.

Examined first instar of: *S. arizonica*.

Hosts Unknown.

Phylogenetics

The six species (two described and four undescribed) here constituting *S. (Aphantorhapha)* are similar in a number of characteristics (see Recognition and Description sections), which in combination suggest that the group is monophyletic. Although a number of external similarities are shared among adults, even in combination they do not exclude all other *Siphona s.l.* species. Only when these external characteristics are coupled with the derived states of the male genitalia can this taxon be interpreted as monophyletic, or even diagnosed.

Two derived states are recognized in the male genitalia. One is the tapered shape of the distiphallus (Fig. 124). The other is the broadened cerci (Fig. 143), which were observed in the single dissections of *S. (A.)* spp. 1-4 and some dissections of *S. arizonica* specimens (*i.e. S. arizonica* with cerci varied from average to broadened). Though the cerci of the single dissected male of *S. atoma* are of average shape, this species is very similar in all other respects to other members of *S. (Aphantorhapha)*. In fact, the short cerci and toothed distiphallus of *S. atoma* suggests it is sister species to *S. arizonica*.

Siphona pulla, described by Reinhard in *Aphantorhapha*, is only known from the female holotype. The type does not agree in all respects with the present concept of *S. (Aphantorhapha)*, and cannot be placed into another supraspecific taxon of *Siphona s.l.* without study of male genitalic characters. *S. pulla* is therefore left as an unplaced species of *Siphona s.l.*

Geographic distribution

The two described species of *S. (Aphantorhapha)* and *S. (A.)* spp. 3 and 4 are primarily southern Nearctic in distribution. *S. arizonica* is the most widely distributed, ranging from Arizona and western New Mexico through Durango, Chihuahua and Oaxaca to San Cristobal, Chiapas. *S. atoma* is only known from the type series collected from College Station, Texas. *S. (A.)* sp. 3 is known from one male collected from Grant Co., New Mexico, and *S. (A.)* sp. 4 from two males collected near La Ciudad, Durango.

Two new species of *S. (Aphantorhapha)* are recognized from the Neotropics. *Siphona (A.)* sp. 1 is known from a single male collected from Ibarra, in the Imbabura province of Ecuador (2200m, 2-4.VI.1977). The other species, *S. (A.)* sp. 2, is known from several specimens collected over several years from Nova Teutonia, SE Brazil.

List of described species included in Siphona (Aphantorhapha)

N,S *arizonica* Townsend, 1919: 586. Holotype male, USA: Arizona, Chiricahua Mtns. (USNM). Holotype examined.

N *atoma* Reinhard, 1947: 19. Holotype male, USA: Texas, College Station (CNC). Holotype examined.

4.17 Siphona (Aphantorhaphopsis Townsend)

Figs. 64, 91-92, 125, 176-181.

Aphantorhaphopsis Townsend, 1926a: 34. Type-species, *A. orientalis* Townsend, 1926 (original designation). **New status** under *Siphona* Meigen.

Asiphona Mesnil, 1954: 9, 10 (as subgenus of *Siphona*). Type-species, *Thryptocera selecta* Pandellé, 1894 (original designation). **New synonym** of *Aphantorhaphopsis* Townsend.

Recognition

This taxon was called *Asiphona* Mesnil previously (e.g. Andersen 1983), but *Aphantorhaphopsis* has date priority and is used here. It comprises a non-monophyletic assemblage of Old World *Siphona s.l.* species not belonging to *Siphona s.s.* or *S. (Çeranthia)*. The rationale for recognizing such an unsatisfactorily-defined group in the formal classification of the Siphonini is explained below in the Phylogenetics section.

Species of *S. (Aphantorhaphopsis)* have a short aristomere 1, lower proepimeral seta undeveloped, lower katepisternal seta at least length of upper anterior one, katepisternum without row of hairs anterior to mid coxa, and anal vein extended to wing margin. These states distinguish *S. (Aphantorhaphopsis)* species from all Old World non-*Siphona s.l.* species.

Siphona s.s. species have a characteristically elongate proboscis, with labella rigid basally and at least as long as the prementum. Most *S. (Aphantorhaphopsis)* species have padlike labella, and are thus easily separated from *Siphona s.s.* species by this state. The labella of few *S. (Aphantorhaphopsis)* species are lengthened, and in very few as long as prementum, but only in Nepal sp. 1 are they also inflexible along basal half (in life) and with reduced number of pseudotracheae as in *Siphona s.s.* species. Nepal sp. 1 is distinguished from *Siphona s.s.* species by its possession of a seta posteriorly on the pregonite (this seta is absent from *Siphona s.s.* species and present in, or absent from, *S. (Aphantorhaphopsis)* species).

S. (Ceranthia) species are characterized by a cylindrical palpus (Fig. 16), long seta posteriorly on the pregonite (Fig. 94) and distinctive shape of the distiphallus (Fig. 127). Two *S. (Aphantorhaphopsis)* species, Australia sp. 1 and New Guinea sp. 1, have a cylindrical palpus like in *S. (Ceranthia)* species, but these do not have the male genitalic states of that taxon (they have a bare pregonite and the distiphallus is not laterally incised).

Description

Length: 3.0-5.0mm.

Head.— Anterior proclinate orbital seta subequal to or longer than posterior one. Eye of male medium-small to large, 0.69-0.89 head height; eye of female smaller than or subequal to eye of male. Flagellomere 1 of male short to medium-long, 0.38-0.63 head height; shape linear to broad in most species, subquadrangular in few. Flagellomere 1 of female subequal or smaller than in male. Aristomere 1 short. Aristomere two 1.5-4X longer than wide. Aristomere 3 long and evenly tapered in most species, short and thickened to near tip in few; almost bare to short plumose. Clypeus narrow and enclosed in membrane to U-shaped. Palpus short and clavate in most species, long in some species with an elongate proboscis, reduced and cylindrical (as in *S. (Ceranthia)* spp.) in Australia sp. 1 and New Guinea sp. 1. Proboscis with prementum short in most species, slightly lengthened to elongate in few; labella padlike in most species, slightly lengthened to subequal prementum length in few with more than basal half flexible in life (*e.g. S. alticola, S. crassulata, S. fera*, Nepal sp. 2 and New Guinea sp. 3), very long and *Siphona*-like (*i.e.* labella inflexible over at least basal half and number of pseudotracheae reduced) in Nepal sp. 1 (proboscis 2.6X head height).

Thorax.— Prosternum setulose, except bare in Nepal sp. 3. Lower katepisternal seta subequal in length to, or longer than, upper anterior seta. Three or four postsutural dorsocentral setae. Upper part of anepisternum with one setula in most species, two in few. Fore tibia with preapical *ad* seta much shorter than *d* seta in almost all species, known to be as long as *d* seta only in *S. laticornis*. Mid tibia with one *ad* seta in most species (short in Australia sp. 1), two *ad* setae in Kenya sp. 1 and South Africa sp. 1. Claws short. Wing vein CuA_1 with distal portion 0.26-1.4X length of proximal portion (mean 0.47). Wing setulae: R_1 dorsally bare or distally setulose, ventrally bare in most species, distally setulose in few; R_{4+5} setulose between base and *r-m* in most species, known to be setulose beyond *r-m* only in Australia sp. 2; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent to strong. T_3-T_5 average or with weak lateral discal setae.

Male genitalia (Figs. 64, 91-92, 125).— S_5 with posterior margins of processes approximately U-shaped in most species, obtusely angled in few, almost V-shaped in Nepal sp. 1 (Fig. 64, resembling typical *Actia* shape except median cleft more distinct); apical lobe distinctly differentiated, apex slightly to markedly curved inward in several species; median lobe narrowly to broadly rounded or truncate, relatively unmodified; processes moderately setulose. T_6 varied from two small lateral sclerites to single, narrow to broad, dorsally continuous sclerite. Hypandrial apodeme lengthened in New Guinea sp. 1, very elongate in Nepal sp. 4. Ejaculatory apodeme with fan-shaped portion 0.5-1.5X wider than hypandrial apodeme. Pregonite (Figs. 91-92) in profile curved anteriorly and pointed apically in most species, in others varied from short and broad to long and thin, in *S. nigronitens* expanded basally and fused with hypandrial apodeme, in Kenya sp. 1 expanded ventrolaterally; bare or with small seta posteriorly in most species, large seta present in *S.* nr. *fera* (absent from holotype of *S. fera*). Epiphallus present or absent. Distiphallus (Fig. 125) reduced posteriorly, markedly varied in profile, laterally incised or complete, apically pointed or rounded or truncate, with or without recurved spines along anterior and/or lateral margin, in about half the species with long posterolateral arm. Postgonite long and pointed in Australia sp. 2, very reduced in *S. nigronitens* and Nepal sp. 4, rounded or truncate in other species. Surstylus markedly varied, short to long, thin to broad, straight to curved posteriorly; basally fused with epandrium in Nepal sp. 4, free from epandrium in other species. Cerci average length and smoothly curved in most species, rather short in few species, slightly inflexed at midlength in few species; moderately setose on basal half.

Examined male genitalia of: *S. alticola, S. brunnescens, S. crassulata, S. fera, S.* nr. *fera, S. nigronitens, S. orientalis, S. starkei, S. xanthosoma*, Australia spp. 1-2, Kenya sp. 1, Nepal spp. 1-4, New Guinea spp. 1-3 and Uganda sp. 1. Examined published figure of: *S. siphonoides* (Andersen 1983, fig. 19).

Female genitalia.— Short. S_6 with average length hairs. T_6 absent (not examined in Australia sp. 1 and Nepal sp. 4); spiracles of segment 6 in membrane dorsal to lateral margins of S_6. S_7 with long anterior apodeme; not keeled posteromedially. T_7 absent from most species, present as two small lateral sclerites in Nepal sp. 1; spiracles of segment 7 in membrane between segments 6 and 7. S_8 distinctly developed, haired, broader than average in few species, large and rather pointed in Australia sp. 1. T_{10} absent from Uganda sp. 1, present as lightly to distinctly sclerotized pair of sclerites or median sclerite in other species. Examined female genitalia of: Australia sp. 1, Kenya sp. 1, Nepal spp. 1,4, South Africa sp. 1 and Uganda sp. 1. Examined published figure of: *S. samarensis* (Andersen 1983, fig. 5).

First instar (Figs. 176-181).— Cephalopharyngeal skeleton: Labrum hatchet-like; oriented forward or slightly downward in most species (Figs. 177-181), curved markedly downward in Australia sp. 1 (Fig. 176). Lateral sclerite unmodified in most species, broad in Australia sp. 1. Hypopharyngeal sclerite unmodified. Both dorsal and ventral cornua present, former relatively short in Australia sp. 1. Australia sp. 1 with external patch of dense scales ventrally below cornua of cephalopharyngeal skeleton.

Posterior abdominal segments of first instar ventrally: Segment 7 with setation varied posteriorly, Australia sp. 1 (Fig. 176) and Nepal sp. 4 (Fig. 179) with two widely spaced hooks, Uganda sp. 1 (Fig. 180) with row of tiny spinules (this species is the only examined *Siphona* species without large spinules or hooks in this position), other species with about four to eight hooks (Figs. 177-178, 181). Segment 8 bare or with one to several rows of minute to small spinules anteriorly; row of small to large uniform-sized spinules posteriorly, with additional row of smaller spinules in some species. Segment 9 bare or with row or median group of small spinules posteriorly; anus average-sized.

Examined first instar of: Australia sp. 1, Kenya sp. 1, Nepal spp. 1,4, South Africa sp. 1 and Uganda sp. 1.

Hosts

Known hosts of *S. (Aphantorhaphopsis)* comprise a diverse assemblage of Macrolepidoptera, as might be expected of a grade-based taxon such as this (Table 2). Five host families are represented, of which two, the Noctuidae and Geometridae, are commonly recorded among other siphonines. The three remaining families, the Hesperiidae, Liparidae and Arctiidae, are virtually unreported as hosts of other siphonines (a single record being that of an arctiid host for *Ceromya bicolor*). One European species, *S. samarensis*, is recorded from an economically important pest, the gypsy moth (*Porthetria dispar*), though its level of parasitism is apparently very low.

Given the possibly polyphyletic nature of *S. (Aphantorhaphopsis)* and the meagre extent to which both its species and hosts are known, the diversity of hosts here recorded is probably far from representative for the taxon.

Phylogenetics

The present grouping of Old World species under *S. (Aphantorhaphopsis)* is one of taxonomic convenience, as too little is known about these species to formulate a phylogenetically-based classification. Adults have the derived features of *Siphona s.l.*, and are assignable within the genus to *S. (Aphantorhaphopsis)* by their lack of the apotypic states defining the other *Siphona* subgenera. It is inferred that this group lacks autapotypies because it is composed of several (numerous?) lineages. This taxon is either paraphyletic or polyphyletic, depending upon the true relationships of these species with those of other *Siphona* subgenera.

The diverse assemblage of species comprising this group can only be adequately reclassified by a thorough study of at least external and male genitalic characters. Even a revision of described species is apt to be inadequate for both classificatory and identification needs, as many undescribed species are known.

The description above of *S. (Aphantorhaphopsis)* is based upon the study of specimens of as many species as were available. Though this characterization of *S. (Aphantorhaphopsis)* is recognized as an interim measure until a thorough revision is undertaken, it is nevertheless useful, as it is the first comprehensive review of the included species. Its concept is the same as that of Andersen's (1983) *Asiphona* Mesnil, over which the name *Aphantorhaphopsis* has priority.

Andersen similarly diagnosed this taxon as a group of Old World siphonines belonging to the *Siphona* lineage and lacking the derived states of the other taxa (in his case *Siphona s.s.* and *S. (Ceranthia)* because his revision dealt strictly with Old World siphonines). Andersen found no autapotypies of *Asiphona*, but retained the taxon as a genus and hypothesized a sister group relationship between it and *Ceranthia*. He based this hypothesis on the shared possession in these taxa of a seta on the posterior surface of the pregonite, which is absent from *Siphona s.s.* species. However, the present study has shown that some species of *S. (Aphantorhaphopsis)* lack this seta and many New World *Siphona s.l.* species possess it, so presence of a seta is not synapotypic of this taxon and *S. (Ceranthia)*. The significance of this seta, with respect to the phylogeny of the supraspecific taxa of *Siphona s.l.*, is discussed in the Evolution chapter.

An attempt was made while revising the supraspecific taxa of *Siphona s.l.* to discover species of *S. (Aphantorhaphopsis)* which might have close New World relatives. None was found, perhaps because New World subgenera are mostly Neotropical and southern Nearctic in distribution and are thus likely to be too old to have easily recognized Old World members, if indeed any exist. It was not clearly established whether or not some of the unplaced *Siphona s.l.* species of the northern Nearctic region are closely related to any Old World *S. (Aphantorhaphopsis)* species, though this is a distinct possibility.

Geographic distribution

S. (Aphantorhaphopsis) as here defined is a possibly polyphyletic assemblage of Old World species. The 21 described species are fairly evenly distributed throughout the Palearctic, Afrotropical and Oriental regions, with six species described from each of the first two regions and eight from the third. Only one species is described from Australia. Examination of material from the Old World indicates that at least several, perhaps many, undescribed species exist in each region, particularly in the Oriental and Australian regions.

The six described Palearctic species are apparently restricted to Europe (Herting 1984 [species included under broad concept of *Ceranthia*]; no records in publications of Richter) and are keyed and redescribed in Mesnil (1963a-1964: 843-853). Species of the other regions are catalogued in Crosskey (1973, 1976a, 1980), mostly in the genus *Ceromya*. Dear and Crosskey (1982) key three species occurring in the Philippines, *S. angustifrons*, *S. orientalis* and *S.* nr. *selangor* (all keyed as *Ceromya* species), and species of central Africa and Madagascar are keyed in Mesnil (1954 and 1977b, respectively).

The distribution of *S. (Aphantorhaphopsis)* species cannot be historically interpreted until the phylogenetic relationships among these species are better known, as well as their relationships with other subgenera of *Siphona*.

List of described species included in Siphona (Aphantorhaphopsis)

O *alticola* (Mesnil), 1953: 110 (*Crocuta* (*Siphona*)). Holotype male, Burma: Kambaiti (ZMU). Holotype examined. **New combination.**

O *angustifrons* (Malloch), 1930b: 131 (*Actia*). Holotype male, Malaysia: Kedah Peak (BMNH). Holotype examined. **New combination.**

P *brunnescens* (Villeneuve), 1921: 46 (*Actia*). Holotype male, German Democratic Republic: Oberlausitz, Niederoderwitz (CNC). Holotype examined. **New combination.**

O *crassulata* (Mesnil), 1953: 112 (*Crocuta* (*Siphona*)). Holotype male, Burma: Kambaiti (ZMU). Holotype examined. **New combination.**

A *fera* (Mesnil), 1954: 26 (*Siphona* (*Asiphona*)). Holotype male, Zaire: Nyongera (MRAC). Holotype examined. **New combination.**

O *laboriosa* (Mesnil), 1957: 48 (*Siphona* (*Asiphona*)). Holotype male, Burma: Kambaiti (ZMU). Holotype examined. **New combination.**

O *laticornis* (Malloch), 1930b: 131 (*Actia*). Holotype male (not female), Malaysia: Selangor (BMNH). Holotype examined. **New combination.**

O *mallochiana* (Gardner), 1940: 178 (*Actia*). Type(s) puparia, India (?FRI). **New combination.**

syn. *perispoliata* (Mesnil), 1953: 108 (*Actia*). Holotype male, China: Canton (BMNH).— Crosskey, 1976a: 213. Holotype examined.

A *nigronitens* (Mesnil), 1954: 25 (*Siphona* (*Asiphona*)). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined. **New combination.**

U *norma* (Malloch), 1929a: 116 (*Actia*). Holotype male, Australia: New South Wales, Como (USNM). Holotype examined. **New combination.**

O *orientalis* Townsend, 1926a: 35. Holotype male, Indonesia: Sumatra, Fort de Kock (ZMA). Holotype examined.

A *picturata* (Mesnil), 1977b: 179 (*Asiphona*). Holotype male, Madagascar: Belazao (MNHN). **New combination.**

A *pudica* (Mesnil), 1954: 27 (*Siphona* (*Asiphona*)). Holotype male, Zaire: Eala (MRAC). Holotype examined. **New combination.**

P *samarensis* (Villeneuve), 1921: 46 (*Actia*). Holotype female, Russia: Kujbyšev [Samara] (CNC). Holotype examined. **New combination.**

O *selangor* (Malloch), 1930b: 132 (*Actia*). Holotype male, Malaysia: Selangor (BMNH). Holotype examined. **New combination.**

P *selecta* (Pandellé), 1894: 112 (*Thryptocera*). Syntypes, France: Var, Hyères (MNHN). **New combination.**

P *siphonoides* (Strobl), 1898: 235 (*Gymnopareia*). Holotype male, Austria: Steiermark, Gesäuse (NMBA). **New combination.**

syn. *brunneipalpis* (Villeneuve), 1921: 45 (*Actia*). Holotype male, Federal Republic of Germany: Harz (CNC).— Mesnil, 1963a: 848. Holotype examined.

A *speciosa* (Mesnil), 1954: 28 (*Siphona* (*Asiphona*)). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined. **New combination.**

P *starkei* (Mesnil), 1952b: 155 (*Actia*). Holotype male, German Democratic Republic: nr. Bautzen, Hennerstadt (CNC). Holotype examined. **New combination.**

P *verralli* (Wainwright), 1928: 208 (*Actia*). Holotype male, Scotland: Sutherlandshire, Mound (HDE). Holotype examined. **New combination.**

A *xanthosoma* (Mesnil), 1954: 28 (*Siphona* (*Asiphona*)). Holotype male, Zaire: Rwindi (MRAC). Holotype examined. **New combination.**

4.18 Siphona (Baeomyia O'Hara)

Figs. 15, 22, 38, 93, 126, 184.

Baeomyia O'Hara, 1984: 1390. Type-species, *Aphantorhapha hurdi* Reinhard, 1959 (original designation). **New status under *Siphona* Meigen.**

Recognition

Adults of *S. (Baeomyia)* species are among the smallest of siphonines, measuring 2-3mm in length. They are only recorded from western North America and are easily recognized among New World siphonines by the absence of an *ad* seta on the mid tibia (Fig.

38) - a state only shared with several Old World *Actia* and *Ceromya s.s.* species. Also diagnostic is the elongate aristomere 1, which is subequal in length to aristomere 2 (Fig. 15; only as long in few Old World siphonines). *S. (Baeomyia)* species are also characterized by padlike labella, three postsutural dorsocentral setae, wing vein R_{4+5} not setulose beyond crossvein *r-m*, anal vein extended to wing margin, and crossvein *dm-cu* far removed from wing margin (Fig. 22).

Description

Length: 2.0-3.0mm.

Head (Fig. 15; also see head profiles in O'Hara 1984, figs. 1-5.).— Anterior proclinate orbital seta subequal in length to posterior one. Eye of male and female subequal, small to medium-large, 0.65-0.83 head height. Flagellomere 1 of male short to medium length, 0.39-0.56 head height; shape average to broadly subquadrangular. Flagellomere 1 of female smaller than in male or subequal in size. Aristomere 1 elongate, subequal in length to aristomere 2, each 2.4-4.6X longer than wide. Aristomere 3 almost bare, very short, evenly tapered or thickened to near tip. Clypeus U-shaped. Palpus short, clavate. Proboscis with prementum short, labella padlike.

Thorax (Fig. 22).— Prosternum bare or sparsely setulose. Lower katepisternal seta shorter than or subequal in length to upper anterior ~~seta. Three postsutural~~ dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia lacking *ad* seta. Claws short. Wing (Fig. 22 and O'Hara 1984, fig. 10): CuA_1 with distal portion 0.64-1X length of proximal portion (*i.e. dm-cu* far removed from wing margin; mean 0.85). Wing setulae: R_1 dorsally bare or with one setula apically on bend, ventrally bare; R_{4+5} setulose between base and *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median or lateral marginal setae. T_3-T_5 with average setation, setae weakly to strongly developed.

Male genitalia (Figs. 93, 126 and O'Hara 1984, figs. 6-9).— S_5 with posterior margins of processes approximately U-shaped; apical lobe distinctly differentiated; median lobe rounded, relatively unmodified; processes sparsely to moderately setulose. T_6 narrow to broad, dorsally continuous. Ejaculatory apodeme with fan-shaped portion 1.0-1.5X wider than hypandrial apodeme. Pregonite (Fig. 93) in profile curved anteriorly, pointed apically; with tiny seta posteriorly (not shown in O'Hara 1984). Epiphallus absent. Distiphallus (Fig. 126) reduced posteriorly, not incised laterally, without enlarged teeth anteriorly or ventrally, in profile apically truncate. Postgonite short to average in size, apically rounded. Surstylus almost straight to sharply curved posteriorly; basally free from epandrium. Cerci short to average length, smoothly curved (O'Hara 1984, figs. 7-9) or sharply inflexed at midlength (O'Hara 1984, fig. 6); moderately setose on basal half.

Examined male genitalia of: *S. hurdi, S. juniperi, S. sonorensis* and *S. xanthogaster* (all shown in O'Hara 1984, figs. 6-9).

Female genitalia.— Short. S_6 with average length hairs. T_6 absent; spiracles of segment 6 in membrane dorsal to lateral margins of S_6. S_7 with long anterior apodeme; not keeled posteromedially. T_7 absent; spiracles of segment 7 in membrane between segments 6 and 7. S_8 distinctly developed, haired. T_{10} absent.

Examined female genitalia of: *S. antennata, S. hurdi, S. sonorensis* and *S. xanthogaster* (all shown in O'Hara 1984, figs. 11-14 [fig. 14, *S. antennata*, mislabelled as *B. juniperi*]).

First instar (Fig. 184).— Cephalopharyngeal skeleton: Labrum hatchet-like. Lateral sclerite not apparent. Hypopharyngeal sclerite unmodified. Both dorsal and ventral cornua present.

Posterior abdominal segments of first instar ventrally: Segment 7 with row of about six to eight spinules posteriorly. Segment 8 with several rows of minute spinules anteriorly; row of small spinules posteriorly. Segment 9 bare posteriorly; anus average-sized.

Examined first instar of: *S. hurdi* and *S. sonorensis*.

Hosts

Hosts of two *S. (Baeomyia)* species are known, and are larvae belonging to the geometrid genus *Semiothisa* (Table 2 and O'Hara 1984).

Phylogenetics

S. (Baeomyia) is a monophyletic taxon based on several synapotypies (see O'Hara 1984: 1388-1389). These include absence of an *ad* seta on the mid tibia (this seta independently lost in few Old World *Actia* and *Ceromya s.s.* species), aristomere 1 subequal in length to aristomere 2 (a rare state present in few, unrelated, Old World siphonines), very small-sized adults, very short aristomere 3 (figs. 1-5 in O'Hara 1984), and crossvein *dm-cu* far removed from wing margin (Fig. 22). The last state is possibly not autapotypic of *S. (Baeomyia)* because it is shared with some other *Siphona s.l.* species (see Table 1); the position of *dm-cu* is such a labile character among siphonines that it is difficult to establish among which lineages its derived state (*i.e.* far removed from wing margin) is synapotypic, and among which it is convergent (O'Hara 1984: 1388).

Geographic distribution

S. (Baeomyia) species are restricted in distribution to western North America. Known distributions are shown and discussed in O'Hara (1984).

List of described species included in Siphona (Baeomyia)

N *antennata* O'Hara, 1984: 1393. Holotype male, USA: Arizona, Graham Co., near Marijilda canyon (CAS). Holotype examined.

N *hurdi* (Reinhard), 1959: 161 (*Aphantorhapha*). Holotype male, USA: California, Panamint Mtns. (CAS). Holotype examined.

N *juniperi* O'Hara, 1984: 1395. Holotype male, Canada: British Columbia, Williams Lake (CNC). Holotype examined.

N *sonorensis* O'Hara, 1984: 1393. Holotype male, USA: Arizona, Graham Co., 2.4km. west on Hwy. 366 from Hwy. 666 (CNC). Holotype examined.

N *xanthogaster* O'Hara, 1984: 1394. Holotype male, Canada: British Columbia, Vermilion (CNC). Holotype examined.

4.19 Siphona (Ceranthia Robineau-Desvoidy)

Figs. 16, 44, 46, 65, 94, 127, 185-187.

Ceranthia Robineau-Desvoidy, 1830: 88. Type-species, *C. fulvipes* Robineau-Desvoidy, 1830 (by designation of Robineau-Desvoidy, 1863: 685) = *Ceromya abdominalis* Robineau-Desvoidy, 1830. New status under *Siphona* Meigen.

Recognition

Members of this subgenus are widely distributed, and with few exceptions are easily recognized. Adults are characterized externally by a cylindrical palpus (Fig. 16), a derived state within the Siphonini. This state is also present in *S. (Aphantorhaphopsis)* Australia sp. 1 and New Guinea sp. 1, but these species do not have *S. (Ceranthia)*-like male genitalia (see below), and seem more closely related to certain species of *S. (Aphantorhaphopsis)*.

Two derived features of the male genitalia are also characteristic of *S. (Ceranthia)* species. The posterolateral margins of the distiphallus are incised to varied degrees, with distinct posterolateral arm (one per side; Fig. 127). In addition, a seta projects posteriorly from the pregonite (Fig. 94), and is larger than in all but very few other *Siphona* species. Atypical in this respect is *S. (Ceranthia)* Mauritius sp. 1, in which this seta is absent. This species possesses a cylindrical palpus and *S. (Ceranthia)*-like distiphallus, and is recognized as a member of this subgenus by these features.

Adult females of *S. (Ceranthia)* species have a posteromedially keeled (Figs. 44, 46) sternum 7, and though this state is not unique to species of this subgenus, it is apparently universal among its members.

Description

Length: 3.0-5.5mm.

Head (Fig. 16).— Anterior proclinate orbital seta subequal in length to posterior one in most species. Eye of male medium-small to large, 0.69-0.88 head height; eye of female usually smaller than in male. Flagellomere 1 of male medium-short to medium-long, 0.42-0.66 head height; shape broad to subquadrangular. Flagellomere 1 of female shorter and narrower than in male. Aristomere 1 short. Aristomere two 2.0-8.0X longer than wide, generally less than 4X. Aristomere 3 almost bare to micropubescent, rather short and evenly tapered. Clypeus varied from narrow and enclosed in membrane to U-shaped. Palpus short or reduced, cylindrical (not apically clavate). Proboscis with prementum short, labella padlike.

Thorax.— Prosternum setulose. Lower katepisternal seta longer than upper anterior seta. Three or four postsutural dorsocentral setae. Upper part of anepisternum with single setula in most species, with two in few. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.30-0.51 length of proximal portion (*i.e. dm-cu* near wing margin; mean 0.42). Wing setulae: R_1 bare dorsally and ventrally in most species, distally setulose dorsally in few, distally setulose dorsally and ventrally in *S. terrosa*; R_{4+5} setulose between base and *r-m* in most species, beyond *r-m* in *S. pallida*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae; lateral marginal setae strong. T_3-T_5 average in most species, with extra pair of lateral marginal setae on T_3 in few species.

Male genitalia (Figs. 65, 94, 127).— S_5 (Fig. 65) little varied; posterior margins of processes approximately U-shaped; apical lobe large and distinctly differentiated, in most species apex curved inward; median lobe rounded, relatively unmodified; processes sparsely to moderately setulose. T_6 narrow to broad, dorsally continuous or narrowly discontinuous. Ejaculatory apodeme with fan-shaped portion 1.0-1.5X wider than hypandrial apodeme. Pregonite (Fig. 94) in profile curved anteriorly, more or less pointed apically; large seta posteriorly (except bare in Mauritius sp. 1). Epiphallus absent. Distiphallus (Fig. 127) reduced posteriorly, laterally incised to form posterolateral arm extended slightly to markedly beyond anterior margin; anterior margin spinulose or toothed. Postgonite apically rounded or truncate. Surstylus straight, extended slightly beyond tip of cerci; basally free from epandrium. Cerci average length, smoothly curved at midlength; moderately setose on basal half.

Examined male genitalia of: *S. abdominalis* (fig. 20 in Andersen 1983, as *Ceranthia fulvipes*), *S. flavipes, S. plorans, S. scutellata*, Ethiopia sp. 1, Mauritius sp. 1 and U.S. spp. 1-5.

Female genitalia (Figs. 44, 46).— Short to elongate (*e.g.* U.S. sp. 7). S_6 with average length hairs, ventrally flat or slightly keeled posteromedially. T_6 absent; spiracles of segment 6 in membrane dorsal to lateral, or anterolateral, margins of S_6. S_7 with long anterior apodeme; distinctly keeled posteromedially, in few species posterior margin narrow and elongate and covering S_8. T_7 absent; spiracles of segment 7 in membrane dorsal to anterolateral margins of S_7. S_8 distinctly developed, haired. T_{10} present as two sclerites.
Examined female genitalia of: *S. abdominalis, S. flavipes* and U.S. spp. 1-7. Examined published figure of: *S. tenuipalpis* (Andersen 1983, fig. 6).

First instar (Figs. 185-187).— Cephalopharyngeal skeleton: Labrum hatchet-like. Lateral sclerite unmodified to large (U.S. sp. 1, Fig. 186). Hypopharyngeal sclerite unmodified in most species, enlarged and attached to lateral sclerite in U.S. sp. 1. Both dorsal and ventral cornua present.

Posterior abdominal segments of first instar ventrally: Segment 7 with row of about six to eight large spinules posteriorly. Segment 8 with one to several rows of minute to small spinules anteriorly; posteriorly with row of about eight to ten large spinules medially and smaller spinules laterally. Segment 9 bare posteriorly; anus rather small.
Examined first instar of: *S. abdominalis, S. flavipes* and U.S. spp. 1-2,4-5,7.

Hosts

The hosts of four *S. (Ceranthia)* species are known, and these all belong to the Geometridae (Table 2).

Phylogenetics

S. (Ceranthia) is a clearly defined, monophyletic lineage of *Siphona s.l.* The cylindrical palpus of adults (Fig. 16) has long been recognized as the distinguishing feature (and synapotypy) of this group, and to this is added two genitalic states which further support monophyly of the subgenus: the distiphallus is characteristically incised posterolaterally, with distinct posterolateral projection (Figs. 127), and the pregonite possesses a large seta posteriorly (Fig. 94). Females possess a posteromedially keeled (Figs. 44, 46) sternum 7, and larvae (so far as known) are parasitic only on larval geometrids, but these characteristics may not be autapotypic of *S. (Ceranthia)* species.

Two species assigned to *S. (Aphantorhaphopsis)* also have a cylindrical palpus - Australia sp. 1 and New Guinea sp. 1. These species do not possess other derived states of *S. (Ceranthia)*, and seem to have developed a cylindrical palpus independently of *S. (Ceranthia)* species. Other characters suggest that they are closely related to species with a normal palpus belonging to the broadly defined *S. (Aphantorhaphopsis)*. With exclusion of these species from *S. (Ceranthia)*, no species of this subgenus are known from the Australian region.

S. (Ceranthia) Mauritius sp. 1 has the derived states of the palpus and distiphallus found in other *S. (Ceranthia)* species, but lacks the large seta on the pregonite which is present in other known species of this taxon. I hypothesize that this seta was present in the groundplan of *S. (Ceranthia)* because at least a small seta is widely distributed among other *Siphona* lineages (Table 1). Therefore lack of this seta from Mauritius sp. 1 is interpreted as a secondary loss.

Geographic distribution

Eight described *S. (Ceranthia)* species are in the Palearctic region, five in the Afrotropical region and one in the Nearctic region. Five of the eight Palearctic species are apparently very limited in distribution, with one each in England (*S. lichtwardtiana*), northern France (*S. tristella*) and Algeria (*S. jocosa*), and two in Japan (*S. japonica* and *S. sulfurea*). More widespread are *S. abdominalis* (common throughout Europe and collected from Mongolia and Chita region (Herting 1973 [as "*Ceranthia* sp. aff. *anomala* Zett." - perhaps a new species], Richter 1975, 1980), *S. tenuipalpis* (described from Berlin, and Zlatoust in the Ural Mtns.) and *S. pallida* (described from Austria, and if correctly identified then also found on the Kuril Islands (Richter 1976b)). A key to the described Palearctic species of *S. (Ceranthia)* is presented in Mesnil (1975: 1399-1400), and distributions are summarized in Herting 1984 (with species of *S. (Aphantorhaphopsis)* included in *Ceranthia*). I have seen specimens of a new Palearctic species from Ethiopia.

Known ranges of the five described Afrotropical *S. (Ceranthia)* species are given in Crosskey (1980). All were described by Mesnil, and their distributions reflect his work on the fauna of the upper Congo area (four species) and Madagascar (one species). I suspect that the *S. (Ceranthia)* fauna of the Afrotropical region is much more diverse than presently recognized.

There are no described *S. (Ceranthia)* species in the Oriental and Australian regions. I have not seen any specimens of *S. (Ceranthia)* species among borrowed Australian siphonines, but examined one female belonging to the subgenus from Coimbatore in southern India (CNC specimen).

The New World *S. (Ceranthia)* are very inadequately known. The single described species, *S. flavipes*, is recorded from eastern Canada and northeastern USA. Approximately six undescribed *S. (Ceranthia)* species occur in North America, and are mostly eastern or western in distribution. The most southern record for *S. (Ceranthia)* in the New World is southwestern New Mexico, USA.

List of described species included in *Siphona* (*Ceranthia*)

P *abdominalis* (Robineau-Desvoidy), 1830: 87. (*Ceromya*). Type(s), France (lost).

  syn. *anomala* (Zetterstedt), 1849: 3213, 3221 (*Siphona*). Two syntypes, Denmark (UZI).— Herting, 1974: 18.

  flavipes Robineau-Desvoidy, 1850: 200. Unjustified emendation of *C. fulvipes* Robineau-Desvoidy, 1830.

  fulvipes Robineau-Desvoidy, 1830: 88. Holotype male, France: Saint Sauveur (lost).— Herting, 1974: 18.

  grisea (Robineau-Desvoidy), 1850: 198 (*Ceromya*). Type(s) male, France: near Paris (lost).— Bezzi and Stein, 1907: 389.

  microcera (Robineau-Desvoidy), 1830: 88 (*Ceromya*). Type(s), France: near Paris (lost).— Mesnil, 1963a: 840.

  vivida (Robineau-Desvoidy), 1850: 196 (*Ceromya*). Types, France: near Paris (lost).— Herting, 1974: 18.

N *flavipes* (Coquillett), 1897: 58 (*Thryptocera*). Holotype female, USA: New Hampshire, White Mtns. (USNM). Holotype examined.

P *japonica* Mesnil, 1963b: 33. Holotype male, Japan: Kyushu (CNC). Holotype examined.

P *jocosa* (Villeneuve), 1942b: 134 (*Actia*). Holotype male, Algeria: Algiers (CNC). Holotype examined.

A *lacrymans* Mesnil, 1954: 24. Holotype male, Zaire: Karisimbi (MRAC). Holotype examined.

P *lichtwardtiana* (Villeneuve), 1931: 61 (as variation of *Actia anomala* (Zetterstedt)). Type, locality not given (ZMHU; not located, maybe lost).

A *livoricolor* Mesnil, 1977b: 178. Holotype female, Madagascar: Anjavidilava (MNHN).

P *pallida* (Herting), 1959: 423 (*Ceranthia* (*Actia*)). Holotype female, Austria: Aflenz, Dorfmeister (NMV). Holotype examined.

A *plorans* Mesnil, 1954: 24. Holotype male, Rwanda: Sabinyo (MRAC). Holotype examined.

A *scutellata* Mesnil, 1954: 22. Holotype male, Zaire: Rweru (MRAC). Holotype examined.

P *sulfurea* Mesnil, 1971: 72. Holotype female, Japan: Hokkaido, Nukabira (CNC).

P *tenuipalpis* (Villeneuve), 1921: 46 (*Actia*). Two male syntypes: Berlin, Federal Republic of Germany and Zlatoust, USSR (CNC). Syntypes examined.

A *terrosa* Mesnil, 1954: 23. Holotype male, Rwanda: Kundhuru (MRAC). Holotype examined.

P *tristella* Herting, 1966: 5. Holotype male, Switzerland: Wallis, Tanay (ETH). Holotype examined.

4.20 Siphona (Pseudosiphona Townsend)

Figs. 17, 66, 95, 128, 140, 188-193.

Pseudosiphona Townsend, 1916: 622. Type-species, *Siphona brevirostris* Coquillett, 1897 (original designation). New status under *Siphona* Meigen.

Recognition

This taxon is one of the more diverse subgenera of New World *Siphona s.l.*, despite the fact that only its type species, *S. brevirostris*, is described. It comprises two species north of Mexico and approximately 16 south of the United States.

Adults of most *S. (Pseudosiphona)* species have a characteristic habitus, distinctive male genitalia, and unique larval cephalopharyngeal skeleton. However, interspecific variation is common and certain species depart from the average condition in one or more states. Because variation from the typical features is particularly prevalent among external characters, and some other *Siphona s.l.* species appear externally similar, examination of male genitalia is essential for the recognition of members of this subgenus. The following diagnosis includes a suite of characteristics shared by most species of *S. (Pseudosiphona)*, though some species deviate from it in one or more states: adults are light colored with mostly yellow legs, light brown thoracic dorsum, and generally heavy pruinosity on the anterior fourth of abdominal terga and very sparse pruinosity over rest of abdomen (in contrast to the more evenly pruinose abdomens of most other New World *Siphona s.l.* species). Head features are markedly varied, but the following combination of states is common to most *S. (Pseudosiphona)* species (Fig. 17): row of short hairs extended from parafrontal to halfway down parafacial, medium-sized flagellomere 1, arista distinctly haired, eye medium-large, and proboscis with labella slightly more than half length of prementum.

S. (Siphonopsis) is a very diverse Neotropical taxon and its members can generally be distinguished externally from those of *S. (Pseudosiphona)* by their more pruinose abdomen, shorter row of parafacial hairs, almost bare arista and slightly longer labella. Some members of these taxa are rather similar despite these differences between most species, but features of the male genitalia reliably separate them.

S. (Pseudosiphona) sp. 15 is the least typical of the subgenus in head characteristics, having an elongate prementum and labella like in *Siphona s.s.* species. The male genitalia of this species deviates slightly from the average condition (described below; not resembling the male genitalia of *S. (Siphona)* species), but features of the first instar confirm its placement here.

The male genitalia of most *S. (Pseudosiphona)* species are very distinctive. In most species the pregonite (Fig. 95) is broadened, anterolaterally spinulose, and has one to several tiny setae posteriorly; possession of all three of these states is apparently unique to *S. (Pseudosiphona)*. In few species the pregonite is more J-shaped. Spinules are present in all examined specimens, but this state is shared with other taxa (though these other taxa have a more slender pregonite). The possession of more than one posterior seta on the pregonite is apparently unique to *S. (Pseudosiphona)* species, though at least one species has only one seta as in some other *Siphona s.l.* species.

The distiphallus of most *S. (Pseudosiphona)* species is unusually uniform in shape (Fig. 128). It is triangular and apically pointed in profile and anterolaterally spined in all but very few species, and this shape is unique to *S. (Pseudosiphona)*. Few species have an apically truncate distiphallus, but these have the typical states of the pregonite.

The cerci of most *S. (Pseudosiphona)* species are sharply inflexed at midpoint (Fig. 140). This state can be seen during external examination of most males and is not present in many other New World *Siphona s.l.* species (see Table 1). This state is not diagnostic of *S. (Pseudosiphona)* since some of its species have smoothly curved cerci.

S. (Pseudosiphona) sp. 15, mentioned above as having a *Siphona s.s.* head habitus, is easily recognized as a *S. (Pseudosiphona)* species by its male genitalia. The pregonite is J-shaped rather than broadened, but has two tiny setae posteriorly as in most other *S. (Pseudosiphona)* species. The distiphallus is of the typical *S. (Pseudosiphona)* shape, though the cerci are smoothly curved in profile.

The cephalopharyngeal skeleton of first instars provides one of the best character states by which to recognize *S. (Pseudosiphona)* species, though is not likely to be routinely examined. The labrum is elongate and hook-like in most species (but not all; Figs. 188-193), and this state is unique to *S. (Pseudosiphona)* species among *Siphona s.l.* species.

Description

Length: 2.0-5.0mm.

Head (Fig. 17).— Proclinate orbital setae subequal in length or anterior one longer. Eye of male medium to large, 0.73-0.86 head height; eye of female slightly smaller to slightly larger than in male. Flagellomere 1 of male short to medium-short, 0.38-0.48 head height; shape rather linear in most species, average to subquadrangular in few. Flagellomere 1 of female subequal or smaller than in male. Aristomere 1 short in most species, as long as wide in at least one species. Aristomere 2 relatively short, 1.5-2X longer than wide. Aristomere 3 short to long and evenly tapered, micropubescent to medium plumose. Clypeus narrow to slightly broadened, enclosed in membrane. Palpus short, clavate. Proboscis with prementum short to elongate (up to head height in length), between 0.5-0.7 head height in most species, labella slightly to moderately lengthened, in most species between 0.6-0.7 prementum length, quite elongate (0.8-1.0 prementum length) with basal half flexible or inflexible in life (latter state *Siphona*-like) in few species.

Thorax.— Prosternum setulose. Lower katepisternal seta subequal in length or longer than upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with one or two setulae. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.36-0.74 length of proximal portion (mean 0.60). Wing setulae: R_1 dorsally bare, or distally or entirely setulose, ventrally bare. R_{4+5} setulose to or beyond *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent from most species, weakly developed in few. T_3-T_5 with average setation.

Male genitalia (Figs. 66, 95, 128, 140).— S_5 (Fig. 66) with posterior margins of processes approximately U-shaped (except almost V-shaped in *S. (P.)* sp. 11, and resembling typical *Actia* shape except median cleft more distinct); apical lobe distinctly differentiated in most species, rather short in *S. (P.)* sp. 19, apex curved inward in few species; median lobe broadly rounded to truncate and relatively unmodified in most species, with accessory lobe slightly developed in few species; processes moderately setulose. T_6 absent or present as two lateral sclerites. Ejaculatory apodeme with fan-shaped portion subequal in width to width of hypandrial apodeme. Pregonite in profile broad along most of length and apically rounded or pointed in most species (Fig. 95), rather J-shaped in few; outer surface short spinose on apical half or less and one to several (in most species several) tiny setae posteriorly. Epiphallus absent. Distiphallus (Fig. 128) reduced posteriorly, not incised laterally, with enlarged spines anterolaterally in almost all species, in profile triangular and apically pointed in most species, subquadrangular and apically truncate in *S. (P.)* spp. 18 and 19, deeply incised anteriorly in most species. Postgonite apically rounded. Surstylus (Fig. 140) varied from average length to elongate, narrow to broad, in most species straight, in few curved posteriorly; basally free from epandrium. Cerci varied from short to elongate, in profile average width to thick and smoothly curved (few species) to sharply inflexed at midlength (most species, Fig. 140); moderately (most species, Fig. 140) to densely (few species) setose on basal half.

Examined male genitalia of: *S. brevirostris, S. (P.)* spp. 1-13,15,17-19.

Female genitalia.— Short to moderately extensible. S_6 with short to long hairs apically, ventrally flat in most species, slightly keeled posteromedially in *S. (P.)* sp. 15, sharply keeled posteromedially in *S. (P.)* sp. 17. T_6 absent; spiracles of segment 6 in membrane dorsal to lateral margins of S_6. S_7 with anterior apodeme rather short in *S. (P.)* sp. 17, long in other species; flat or slightly to markedly keeled posteromedially, average length to elongate, in *S. (P.)* sp. 1 elongate and posteromedially pointed and keeled. T_7 absent or present as two tiny to small lateral sclerites; spiracles of segment 7 in membrane between segments 6 and 7 in most species, in membrane dorsal to posterior margin of S_6 in *S.*

(P.) sp. 17. S_9 distinctly developed, almost bare in *S. (P.)* sp. 3, with thick setae in *S. (P.)* sp. 17, average setation in other species. T_{10} present as median sclerite or paired sclerites. Examined female genitalia of: *S. (P.)* spp. 1-4,14-17.

First instar (Figs. 188-193).— Cephalopharyngeal skeleton: Labrum varied from hook-like to parallel-sided dorsoventrally and apically truncate. Lateral sclerite small to large, apparently absent from *S. (P.)* sp. 16 (Fig. 192). Hypopharyngeal sclerite unmodified to elongate and attached to posterior edge of lateral sclerite. Both dorsal and ventral cornua present, former directed more posteriorly than in most other siphonines.

Posterior abdominal segments of first instar ventrally: Segment 7 with setation varied posteriorly, *S. (P.)* sp. 2 with two widely spaced hooks (Fig. 189), *S. (P.)* sp. 17 (Fig. 193) and sp. 16 (Fig. 192) with four hooks, former with small basal protrusions, latter with basal plates and additional spinules, other species with row of about four to eight hooks (Figs. 188, 190-191). Segment 8 with several rows of minute to small spinules anteriorly; several rows of tiny to small spinules posteriorly in most species, *S. (P.)* sp. 17 with indistinct plates bearing several tiny spinules each, *S. (P.)* sp. 16 with four distinct plates bearing several spinules each. Segment 9 bare or almost so posteriorly; anus small to average-sized.
Examined first instar of: *S. (P.)* spp. 1-2,4,14-17.

Taxonomic changes

Lectotype designation for Siphona brevirostris Coquillett

Siphona (Pseudosiphona) brevirostris was described in *Siphona s.s.* by Coquillett in his "Revision of the Tachinidae" (1897: 76). In that work Coquillett routinely published USNM type numbers for his new species and appropriately labelled his holotypes in the collection (see general discussion of Coquillett's type designations near the beginning of the Classification chapter). Coquillett's type series of *S. brevirostris* consists of three specimens (two females and one male - not three females as published), two of which (both females) were attached to the same pin. The pin with the male specimen bears a paratype label and the other pin, with the two females, bears a type label and a handprinted Townsend label: "Pseudosiphona brevirostris Coq. Gnt. mss." [Gnt. = Genotype, referring to Townsend's selection of *S. brevirostris* as type species of *Pseudosiphona* Tnsd.]. It is evident that both Coquillett and Townsend intended one of the females on the double-mounted pin to be the holotype of *S. brevirostris*, but it is not clear which one. It seems appropriate to consider all three specimens as syntypes, and to select one of the females as lectotype. Accordingly, the two female specimens have been removed to separate pins and one selected, and here designated, lectotype of *Siphona brevirostris* Coquillett. A red bordered label has been attached to the pin bearing the lectotype, and reads: "LECTOTYPE/ Siphona/ brevirostris Coq./ O'Hara designation" (the diagonal slashes indicate separate lines on label). The lectotype also bears the following labels: (1) From Miss/ Murtfeldt, (2) 6, (3) Type/ No. 3574/ U.S.N.M. [red USNM label], (4) Siphona/ brevirostris/ Coq. [Coquillett's handprinted label], (5) Pseudosiphona/ brevirostris Coq./ Gnt. mss. [Townsend's handprinted label]. The lectotype is pinned with a minuten dorso-ventrally through the thorax, and is in good condition except for loss of the right mid leg and tarsi of the left mid and hind legs. The remaining two specimens of the type series, a male and female, are labelled as paralectotypes.

Hosts

Two new host records are known for *S. (Pseudosiphona)*, based on label data accompanying adult specimens in the USNM: one from caterpillars of a lycaenid butterfly (collected in Costa Rica), and the other from larvae of *Chloropteryx* sp. (collected in Trinidad) (Table 2).

Arnaud (1978) records *Siphona brevirostris* from *Oidaematophorus homodactylus* (Table 2), citing the work of Schaffner (1959). This record is probably in error because specimens of *S. brevirostris* are extremely scarce in collections, and their proper identification is very difficult (so few identified specimens are known that comparison with type specimens is almost essential for reliable determination - see discussion concerning the geographic distribution of *S. brevirostris* below).

Phylogenetics

Most *S. (Pseudosiphona)* species have a characteristic habitus (see Recognition section), but some species deviate from it and few other *Siphona s.l.* species approximate it, so no external synapotypies of *S. (Pseudosiphona)* are proposed here. Other character states, in the male genitalia and first instar, provide better evidence for monophyly of this group.

Two structures of the male genitalia, the pregonite and distiphallus, have states unique to *S. (Pseudosiphona)* species. Three characters are recognized on the pregonite: shape, presence or absence of spinules anterolaterally, and presence or absence of a seta(e) posteriorly. Though spinules are on the pregonite of all examined *S. (Pseudosiphona)* species, their presence in some other New World *Siphona s.l.* species indicates this state is not autapotypic of this subgenus. States for the other two characters are unique to *S. (Pseudosiphona)* and are interpreted as synapotypies. The first is the characteristically broadened shape of the pregonite, and the second is the presence of more than one seta posteriorly. Few *S. (Pseudosiphona)* species lack one or the other of these states, but not both. A triangular and anterolaterally spined distiphallus (Fig. 128) is hypothesized as another synapotypy of *S. (Pseudosiphona)* species. The few species which depart from this shape are interpreted as derived for this character as they have the derived states of the pregonite.

A striking apotypy of first instars of *S. (Pseudosiphona)* species is the elongate, hook-like, labrum of most examined species (Figs. 188-193). This state is unique within *Siphona s.l.*, and seems convergent with the somewhat similar labrum of *Ceromya silacea* (Fig. 160) and *Peribaea* species (Figs. 172-175). First instars of at least two *S. (Pseudosiphona)* species (spp. 1 and 16, Figs. 188 and 192) have an apically truncate labrum. Adults of the former species have all the derived states of the male genitalia cited above, so its labrum is interpreted as secondarily broadened. The male of *S. (Pseudosiphona)* sp. 16 is not known, but this species is also considered to have a secondarily broadened labrum because the elaborate spines posteriorly on the ventral surface of the abdomen have more primitive counterparts in *S. (Pseudosiphona)* sp. 17 (Fig. 193) - a species with a hook-like labrum. Therefore a hook-like labrum is hypothesized as a groundplan state and synapotypy of *S. (Pseudosiphona)*.

Geographic distribution

Siphona (Pseudosiphona) is primarily a Neotropical group, for which I am aware of only two species north of Mexico: *S. brevirostris* and undescribed species *S. (P.)* sp. 3. The known range of the latter is from California to east Texas, and southward into northcentral Mexico. The range of *S. brevirostris* is not well documented because of a paucity of collected specimens and a problem with the location of the type locality. The type locality is cited by Coquillett (1897) as Kirkwood, Missouri, but Sabrosky and Arnaud (1965) consider the type locality to be Rhode Island because one of the syntypes bears a label inscribed with "In box with micro-larvae from R.I.". Perhaps Sabrosky and Arnaud are correct, as the only unquestionably conspecific specimen of *S. brevirostris* that I examined was collected in 1983 near Durham in Strafford Co., New Hampshire (CNC). A possibly conspecific specimen (unforunately a female and hence less easily identified) was collected from southwestern New Mexico (USNM). From such information it is apparent that *S. brevirostris* is at least present in northeast USA, and may range southwestward to Missouri or even New Mexico.

Of the other approximately 16 undescribed species of *S. (Pseudosiphona)* known to me, all are Neotropical, with greatest diversity in Chiapas (Mexico), southeastern Brazil, and southern Peru (this pattern is due at least in part to collecting bias). Several species seem to have very wide ranges, extending from Middle America to southeastern Brazil. Unworked material includes specimens from Colombia, Venezuela, British Guiana, Bolivia, and the Caribbean islands of Trinidad and Jamaica. Records from southeastern Brazil and northern Argentina mark the known southern distributional limit of *S. (Pseudosiphona)* species.

List of described species included in Siphona (Pseudosiphona)

N *brevirostris* (Coquillett), 1897: 76 (*Siphona*). Lectotype female (by designation in text), USA: Missouri, Kirkwood (USNM). Lectotype examined.

4.21 *Siphona* (*Siphona* Meigen)

Figs. 25-26, 28, 32, 34, 36, 43, 45, 67, 96, 129, 141, 144, 196-198.

Crocuta Meigen, 1800: 39. Type-species, *Musca geniculata* De Geer, 1776 (by designation of Coquillett, 1910: 528). Suppressed by I.C.Z.N., 1963: 339 (Opinion 678).

Siphona Meigen, 1803: 281. Type-species, *Musca geniculata* De Geer, 1776, by designation of I.C.Z.N., 1974: 157 (Opinion 1008).

Bucentes Latreille, 1809: 339. Type-species, *B. cinereus* Latreille, 1809 (monotypy) = *Stomoxys minuta* Fabricius, 1805.

Phantasiosiphona Townsend, 1915: 93. Type-species *P. tropica* Townsend, 1915 (original designation).

Recognition

Siphona geniculata is the type species of *Siphona s.s.*, and its name literally means "geniculate siphon". The name refers to the long prementum and labella of that species, but it could just as accurately have been applied to any *Siphona s.s.* species, as all are characterized by a long proboscis, with the labella at least as long as the elongate prementum. This state has generally been regarded as unique to *Siphona s.s.* species, but is shared with some other siphonines.

Many non-*Siphona s.s.* species have slight to moderate elongation of the labella, but only in few are they as long as the prementum. These can be discerned as non-*Siphona s.s.* species by the characteristics they share with other siphonine lineages. The several *Actia* species of this type are easily recognized by their row of katepisternal hairs and the anal vein not extended to the wing margin. The few species of *S. (Aphantorhaphopsis)* with the labella almost as long as, to slightly longer than, the prementum have fully flexible labella (not inflexible on basal half in life as in *Siphona s.s.* species) and/or a seta posteriorly on the pregonite (absent from *Siphona s.s.* species). *S. (Aphantorhaphopsis)* Nepal sp. 1 has a very long proboscis of the typical *Siphona s.s.* appearance and is the most easily misplaced species of this taxon, but can be correctly placed by its seta on the pregonite. The proboscis of *S. (Pseudosiphona)* sp. 15 is also *S. (Siphona)*-like, and several other Neotropical species of that subgenus approach this state, but these species are readily recognized by characters in the male genitalia (see Recognition section of *S. (Pseudosiphona)*). The few species of Neotropical *Siphona s.l.* species in which the labella approach the *Siphona s.s.* condition are recognized by the presence on the pregonite of a seta posteriorly and/or spinules apically.

Description

Length: 2.5-6.5mm (rarely less than 3.0mm).

Head (Figs. 25-26; ten Palearctic species shown in Mesnil 1965, figs. 150-159; North American species shown in O'Hara 1983a, figs. 1, 18-59).— Proclinate orbital setae weak to strong, subequal in length or anterior orbital longer. Eye of male small to very large, 0.62-0.91 head height; eye of female smaller than in male. Flagellomere 1 of male markedly varied in length, 0.40-0.75 head height; linear to large and almost triangular. Flagellomere 1 of female smaller than in male. Aristomere 1 short in most species, 1-2X longer than wide in some species with long flagellomere 1, 3X longer than wide in *S. trichaeta*. Aristomere 2 varied from 2.0-10.0X longer than wide, (most species between 2.5-6.0). Aristomere 3 almost bare to micropubescent, long and evenly tapered in most species, short and thickened to near tip in few. Clypeus narrow and enclosed in membrane. Palpus long, clavate. Prementum and labella each slender and elongate; latter at least as long as prementum, inflexible on basal half or more, with pseudotracheae concentrated apically and reduced in number. Proboscis length (prementum + labella) varied from 1.3-4.8X head height (most species between 2.0-3.0).

Thorax (Figs. 28, 32, 34, 36).— Prosternum setulose or bare, varied within some species. Lower katepisternal seta longer than upper anterior seta in most species (Fig. 32), subequal in length to it in very few. Three or four postsutural dorsocentral setae. Upper part of anepisternum with single setula in most species (Fig. 32), with two in few. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Tarsomeres normal in size in most species, tarsomere 5 of fore leg slightly to moderately broadened in females of very few; claws short in most species, medium to large in few. Wing vein CuA_1 with distal portion 0.26-0.67 length of proximal portion (*i.e. dm-cu* near wing margin; mean 0.41). Wing setulae: in most species R_1 dorsally bare or with one or two setulae distally, in very few entirely setulose; ventrally bare (most species) or distally setulose (very few); R_{4+5} setulose between base and *r-m* in most species, beyond *r-m* in few; CuA_1 bare in almost all species, with setulae in very few (*e.g. S. lutea* and *S. bevisi*).

Abdominal terga 1-5.— Abdomen ovoid in shape in most species, markedly elongate in several Afrotropical species. T_{1+2} with or without median marginal setae (present primarily in members of *S. minuta* group - see O'Hara 1983a: 323-4 [as *S. geniculata* group]); one pair (rarely two pair) strong lateral marginal setae in most species, weak or absent in few (weak or absent primarily in *S. maculata* group - see O'Hara 1983a: 321-322). T_3-T_5 average in most species, with extra pair of lateral marginal setae on T_3 in few species.

Male genitalia (Figs. 67, 96, 129, 141, 144).— S_5 little varied (Fig. 67; also Andersen 1982, figs. 3-5), posterior margins of processes approximately U-shaped in most species, obtusely angled in few; apical lobe distinctly differentiated, in very few species apex curved inward (known only in *S. cuthbertsoni*, *S. mesnili* (Andersen 1982, fig. 4) and *S. oligomyia*, (O'Hara 1983a, fig. 11)); median lobe rounded, relatively unmodified; processes sparsely to moderately setulose. T_6 thin to broad and dorsally continuous in most species, almost absent from few (apparently not reduced to two lateral sclerites as in some other siphonines). Ejaculatory apodeme with fan-shaped portion 1.0-2.0X wider than hypandrial apodeme. Pregonite (Fig. 96) in profile little varied, curved anteriorly and more or less pointed apically; bare. Epiphallus absent. Distiphallus (Fig. 129) reduced posteriorly, spined anterolaterally in few species, in profile apically rounded, truncate or pointed posteriorly; laterally incised in very few species (*e.g.* Philippines sp. 1). Postgonite apically rounded. Surstylus (Fig. 141, 144) average length to slightly elongate, more or less straight; basally free from epandrium. Cerci (Fig. 141, 144) average length, smoothly curved at midlength; moderately setose on basal half.

Examined male genitalia of: *S. akidnomyia, S. brunnea, S. collini, S. confusa, S. cuthbertsoni, S. flavifrons, S. futilis, S. geniculata, S. illinoiensis, S. ingerae, S. intrudens, S. kairiensis, S.*

longissima, S. lurida, S. lutea, S. macronyx, S. maculata, S. medialis, S. minuta, S. multifaria, S. nigricans, S. oligomyia, S. pacifica, S. paludosa, S. pauciseta, S. pisinnia, S. rizaba, S. setosa, S. tropica, S. unispina, Ecuador spp. 1-3, Kenya spp. 1-2, Nepal sp. 1, Philippines sp. 1 and Taiwan sp. 1. Examined published figures of: *S. hungarica* (Andersen 1984, figs. 1-3), *S. kairiensis* (O'Hara 1983b, figs. 3-5), North American *Siphona* species (O'Hara 1983a, figs. 60-80), and European *Siphona* species (aedeagus only, Andersen 1982, figs. 2, 18-28, and Andersen 1983, fig. 21). Male reproductive system of *S. geniculata* (as *S. cristata*) shown in Andersen (1983, fig. 1).

Female genitalia (Figs. 43, 45).— Short. S_6 with average length hairs. T_6 absent; spiracles of segment 6 in membrane dorsal to anterolateral margins of S_6. S_7 with long anterior apodeme; not posteromedially keeled. T_7 absent; spiracles of segment 7 in membrane dorsal to anterolateral margins of S_7. S_8 distinctly developed, haired. T_{10} absent or very slightly sclerotized.

Female genitalia of *S. melanura* (examined externally but not dissected) are uniquely modified, in marked contrast to the conservative features in other members of the subgenus. S_6 is longer than wide, shovel-like, extremely smooth and shiny black, apically rounded, with hairs confined to single row on membrane along posterior edge of sternum. S_6 in form of flap-like covering over similarly-shaped, apically more sharply-rounded, blade-like S_7. Examined female genitalia of: *S.* nr. *intrudens, S. lutea, S. maculata, S. nigricans, S. pisinnia* and *S.* nr. *tropica*. Examined published figures of: *S. hungarica* (Andersen 1983, fig. 4), *S. nigricans* (fig. 12 in O'Hara 1983a, as *S. hokkaidensis*) and *S. setosa* (Andersen 1982, fig. 6, and Andersen 1983, fig. 7). Female reproductive system of *S. ingerae* shown in Andersen (1983, fig. 2).

First instar (Figs. 196-198).— Cephalopharyngeal skeleton: Labrum hatchet-like, though smaller than average in *S. nigricans* (Fig. 197). Lateral sclerite unmodified. Hypopharyngeal sclerite unmodified. Both dorsal and ventral cornua present.

Posterior abdominal segments of first instar ventrally: Segment 7 with about four hooks posteriorly. Segment 8 with uneven row of tiny spinules anteriorly; one row of spinules posteriorly, five or six spinules larger than rest in some species. Segment 9 with median group of spinules posteriorly; anus small to average-sized.

Examined first instar of: *S. lutea, S. nigricans* and *S. (Siphona)* sp. 1. First instar of *S. confusa* shown in Andersen (1983, fig. 27).

Taxonomic changes

Siphona nigrohalterata Mesnil

Among the new siphonines described by Mesnil in his 1959 paper about tachinids of East Africa were *Siphona amplicornis amplicornis* and *Siphona amplicornis nigrohalterata* (pp. 21-22). The types (both male) were collected from West Kibo, Nigeria - the former at 2800m between 17-22.IV.1952 and the latter at 3500m between 23-30.IV.1952. These "subspecies" do not seem to be geographically or temporally isolated, as a paratype of *S. a. amplicornis* bears the same locality data as the type of *S. a. nigrohalterata*. I infer from this that these sympatric "subspecies" either freely interbreed (*i.e.* cannot be regarded as separate subspecies) or are reproductively isolated (*i.e.* represent two species). Examination and comparison of the holotypes suggest the latter; the type of *S. a. nigrohalterata* has a slightly longer proboscis, less elongate abdomen, shorter abdominal setae, and markedly different coloration (particularly on the abdomen). These differences are not major, but in total are not atypical of closely related *Siphona* species. Thus I conclude that *S. nigrohalterata* is probably a valid species reproductively isolated from *S. amplicornis*.

Synonymy of Siphona janssensi (Mesnil) with Siphona cuthbertsoni Curran

S. cuthbertsoni is more easily recognized than most African *Siphona* species because of its very large eye, rather short flagellomere 1, proboscis length less than 2.5X head height, and generally dark color (including abdomen entirely dark in ground color). It is probable that Mesnil was unfamiliar with this species of Curran's, except perhaps by name, as he did not mention it in his work about the *Siphona* of the "Belgian Congo".

Specimens of *S. cuthbertsoni* identified by direct comparison with the male holotype of that species were later compared with the male holotype of *S. janssensi*. On the basis of these comparisons, the name *S. janssensi* is here synonymized with that of *S. cuthbertsoni*.

Note about use of the subspecific category

Subspecies have rarely been described in the Siphonini, though Mesnil occasionally used this category for taxa displaying slight morphological differences. Mesnil's concept of subspecies was not based on geographic (and hence I assume not reproductive) isolation. I examined the types of most of Mesnil's subspecies and have reclassified their names as synomyns or separate species. However, I was unable to examine the types of several subspecies of *Siphona fuliginea* Mesnil and *Siphona reducta* (Mesnil). I leave these taxa as classified by Mesnil pending study of the types.

Status of Siphona unispina (Mesnil) and Siphona unispina infuscata (Mesnil)

In 1952 Mesnil revised the *Siphona* species of the "Belgian Congo", naming many new species and one pair of subspecies: *S. unispina unispina* and *S. unispina infuscata* (Mesnil 1952a). As was Mesnil's practice, these subspecies were recognized exclusively on morphological criteria without the now standard requirement of at least partial spatial or temporal separation. Type localities of these taxa are separated by less than 150km, with paratypes of both collected at one intermediate locality. This suggests that the subspecific category is inappropriate, and that the names *S. u. infuscata* and *S. unispina* are synonyms or *S. u. infuscata* is specifically distinct. Crosskey (1980) chose the former, but upon comparison of the types of both taxa I have decided to recognize *Siphona infuscata* as a valid species, based upon three characteristics that differ between the types: 1) proboscis length of *S. unispina* is 3.5X head height as compared with 4.3X head height in *S. infuscata*, 2) thorax of *S. unispina* is bluish gray, in *S. infuscata* mostly brown, and 3) R_{4+5} is setulose beyond *r-m* in *S. unispina* and not beyond *r-m* in *S. infuscata*. Abdominal characteristics and especially male genitalia cannot be compared between types because the abdomen of the type of *S. unispina* is missing. Paratypes were not examined, but a male specimen from the Bwamba river area (SE Zaire) identified by Mesnil as *S. unispina* fits the description of that species and possesses the three characteristics listed above for distinguishing *S. unispina* from *S. infuscata*.

Hosts

Most hosts of *Siphona s.s.* are species of the Noctuidae, and all known lepidopteran hosts belong to the Macrolepidoptera (Table 2). Some members of the *S. geniculata* group are parasites of crane fly larvae (Tipulidae), and are unique in this habit in the Siphonini and among the few tachinids that parasitize other Diptera.

Phylogenetics

The long, geniculate proboscis of *Siphona s.s.* species, with labella at least as long as the elongate prementum, is synapotypic of the subgenus. Elongation of the proboscis has occurred independently in many siphonine lineages, but only in *Siphona s.s.* species are the labella rigid (in life) on basal half or more and at least as long as the prementum in all species. Hence this condition is considered the groundplan (and synapotypic) state of *Siphona s.s.*, and a shorter (with few exceptions padlike) labella the groundplan state of other siphonine lineages.

Andersen (1983) also considered the reduced number of pseudotracheae in *Siphona s.s.* species as a synapotypy of the subgenus, but this state is not treated separately here because for many species it is (in siphonines) directly correlated with elongation of the labella. For example, padlike labella may have about 15 pair of pseudotracheae, elongate labella of *S. (Siphonopsis)* species (Fig. 18) about eight pair, and the long labella of *Siphona s.s.* species about four pair. This correlation is not constant as certain species of *S. (Aphantorhaphopsis)*, for instance, with elongate labella have relatively numerous pseudotracheae. The trend is nevertheless evident, and because of this the number of pseudotracheae on the labella is not treated as a separate character in this study. No other synapotypies of *Siphona s.s.* species are known. The included species have a number of shared characteristics, of which male genitalic similarities are particularly marked (see figs. 60-80 in O'Hara 1983a), and these are congruent with the hypothesis of monophyly of this group. The few other siphonines with a *S. (Siphona)*-like proboscis are recognized as a non-member of that group by synapotypies they share with other taxa, and their non-*S. (Siphona)*-like male genitalia.

Andersen's (1982) revision of European *Siphona s.s.* species went to press at about the time I completed a revision of the North American *Siphona s.s.* species (O'Hara 1983a). Therefore my comparison of Nearctic and Palearctic species of *Siphona s.s.*, and discussion of species groups, did not include the four new European *Siphona s.s.* species described by him. Here I briefly mention the species groups to which Andersen's species belong: *S. ingerae* is a member of the *S. maculata* group, and is closely related to the North American species *S. intrudens*; *S. martini* is now considered conspecific with *S. nigricans* (Andersen, pers. comm.), and is a member of the *S. minuta* group (formerly called the *S. geniculata* group until the name *S. geniculata* was reapplied as senior synonym of *S. cristata*); and *S. mesnili* and *S. variata* are placed in the *S. geniculata* group (formerly called the *S. cristata* group), because these species were considered by Andersen (*op. cit.*) to be close to *S. confusa*. Andersen's new species from Hungary, *S. hungarica* (Andersen 1984), is closely related to *S. ingerae* and *S. intrudens*, and belongs to the *S. maculata* group.

Geographic distribution

Siphona s.s. is widely distributed, with 84 described species. Forty-one of these are Afrotropical in distribution (see Crosskey 1980 for ranges; partial key in Mesnil 1952a), with more species recorded from Madagascar than any other siphonine taxon (Mesnil 1977a). Three apparently endemic species are on Madagascar and five species are shared with the mainland (Crosskey 1980), suggesting that *Siphona s.s.* includes some markedly vagile members. This suggestion is further evidenced by the presence of *Siphona s.s.* species on the Juan Fernández Islands west of Chile, the Canary Islands, and four species with Holarctic distributions (excluding *S. minuta*, introduced by man to North America). It is therefore rather surprising that *Siphona s.s.*, with 41 species in the Afrotropical region and 20 in the Palearctic region, has only three described species in the Oriental region (Crosskey 1976a) and one in the Australian region (O'Hara 1983b). From examined material (and Shima, pers. comm.), the Oriental region and probably islands of the Indoaustralian archipelago north of Australia contain at least a modest number of undescribed species. There is as yet no indication of more than one *Siphona s.s.* species in Australia.

Palearctic *Siphona s.s.* species are best known in England (Crosskey 1976b) and Europe, and are keyed in Mesnil (1964) and Andersen (1982). Additional records are cited in Mesnil and Pschorn-Walcher (1968), Herting (1968b, 1969b, 1973), Draber-Mońko (1978, 1981), Kugler (1979), Richter (1971, 1975, 1976a,b, 1980), Richter and Khitsova (1982), Chao and Shi (1982) and Rognes (1986), and distributions are summarized in Herting (1984).

Twenty-one *Siphona s.s.* species are in North America (including "Middle America"). These were recently revised and their distributions discussed in O'Hara (1983a). Only two exclusively South American *Siphona s.s.* species are described, but there are specimens of at least ten undescribed species among material I have examined.

List of described species included in Siphona (Siphona)

A *abbreviata* (Villeneuve), 1915: 199 (*Bucentes*). Female syntypes, Madagascar: Sikora (NMV). Syntypes examined.

N,S *akidnomyia* O'Hara, 1983a: 311. Holotype male, Mexico: Chiapas, Mt. Zontehuitz (CNC). Holotype examined.

A *albocincta* (Villeneuve), 1942a: 55 (*Bucentes*). Holotype female, Zaire: Nylragongo (CNC). Holotype examined.

A *amoena* (Mesnil), 1952a: 12 (*Crocuta*). Holotype male, Zaire: Karisimbi (MRAC). Holotype examined.

A *amplicornis* Mesnil, 1959: 21. Holotype male, Tanzania: West Kibo (SMNS). Holotype examined.

A *angusta* Mesnil, 1959: 22. Holotype male, Tanzania: West Kibo (SMNS). Holotype examined.

A *antennalis* (Mesnil), 1952a: 9 (*Crocuta*). Holotype male, Zimbabwe: Salisbury (CNC).

A *atricapilla* Mesnil, 1959: 20. Holotype male, Tanzania: West Kibo (SMNS). Holotype examined.

A *bevisi* Curran, 1941: 7. Holotype male, South Africa: Natal, Durban (AMNH). Holotype examined.

A *bilineata* (Mesnil), 1952a: 10 (*Crocuta*). Holotype male, Rwanda: Niabirehe (MRAC). Holotype examined.

P *boreata* Mesnil, 1960: 190. Holotype male, Federal Republic of Germany: Arnsberg (CNC). Holotype examined.

S *brunnea* O'Hara, 1983a: 308. Holotype male, Mexico: Chiapas, Mt. Zontehuitz (CNC). Holotype examined.

A *capensis* Curran, 1941: 7. Holotype female, South Africa: East London (PPRI). Holotype examined.

P *collini* Mesnil, 1960: 188. Holotype male, Great Britain: Cambridgeshire, Burwell (HDE). Holotype examined.

P *confusa* Mesnil, 1961: 201. Holotype male, Sweden: Gränna (CNC). Holotype examined.

A *cothurnata* (Mesnil), 1952a: 17 (*Crocuta*). Holotype male, Rwanda: Burambi (MRAC). Holotype examined.

A *creberrima* (Speiser), 1910: 142 (*Crocuta*). Syntypes, Tanzania: Kilimanjaro (NRS). Syntypes examined.

A *cuthbertsoni* Curran, 1941: 7. Holotype male, Zimbabwe: Salisbury (AMNH). Holotype examined.

  syn. *janssensi* (Mesnil), 1952a: 4 (*Crocuta*). Holotype male (abdomen missing), Rwanda: Kibga (MRAC). Holotype examined. New synonymy.

P *efflatouni* Mesnil, 1960: 188. Holotype female, Egypt: Mariout (CNC). Holotype examined.

P *flavifrons* Staeger *in* Zetterstedt, 1849: 3211. Lectotype female (by designation of Andersen, 1982: 167), Denmark: North East Zealand, Ordrup (ZMUC). Lectotype examined.

N *floridensis* O'Hara, 1983a: 288. Holotype male, USA: Florida, Orlando (AMNH). Holotype examined.

O *foliacea* (Mesnil), 1953: 113 (*Crocuta* (*Siphona*)). Holotype male, Burma: Kambaiti

(ZMU). Holotype examined.

A *fuliginea* Mesnil, 1977a: 77. Holotype male, Madagascar: Ambatolahy (MNHN).

ssp. *cerina* Mesnil, 1977a: 76. Holotype male, Madagascar: Amber Mtn. (MNHN).

rubea Mesnil, 1977a: 77. Holotype male, Madagascar: Manjakatompo (MNHN).

N,S *futilis* Wulp, 1890: 125. Lectotype male (by designation of O'Hara, 1983a: 305), Mexico: Guerrero, Omilteme (BMNH). Lectotype examined.

syn. *ceres* (Curran), 1932: 14 (*Bucentes*). Holotype female, Guatemala: Antigua (AMNH).— O'Hara, 1983a: 305. Holotype examined.

O *gedeana* Wulp, 1896: 109. Holotype female, Indonesia: Java, Goenoeng Gedeh (lost, see Crosskey, 1976a: 214).

syn. *nigripalpis* (de Meijere), 1924: 223 (*Bucentes*). Lectotype male (by designation of Crosskey, 1969: 89), Indonesia: Java, Pangrango (ZMA). Lectotype examined.

P,N *geniculata* (De Geer), 1776: 38 (*Musca*).[2] Three syntypes, Sweden (NRS; types erroneously listed as lost in Andersen 1982 and O'Hara 1983a). This new interpretation of *S. geniculata* as senior synonym of *S. cristata* follows a recent study of the types by Andersen (pers. comm.).

syn. *chaetolyga* Rondani, 1865: 194 (as *chetoliga*). Holotype female, Italy (MZF).— Herting, 1969a: 192.

cristata (Fabricius), 1805: 281 (*Stomoxys*). Holotype female, Denmark: Zealand (ZMUC).— Andersen (pers. comm.). Holotype examined.

palpina Zetterstedt, 1859: 6064. Holotype female, Sweden: Lindholmen (UZI).— Mesnil, 1964: 861.

A *gracilis* (Mesnil), 1952a: 13 (*Crocuta*). Holotype male (head missing), Rwanda: Kibga (MRAC). Holotype examined.

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[2] Page 20 is cited by various authors for the description of *S. geniculata*, but this apparently refers to the German translation of De Geer's work by Goeze in 1782 (Herting, *in litt.*).

P *grandistylum* Pandellé, 1894: 108. Holotype male, France: Pyrenees (MNHN).

P *griseola* Mesnil, 1970: 118 (as subspecies of *S. maculata* Staeger). Holotype male, Israel: Tel Aviv (CNC). Holotype examined.

P *hungarica* Andersen, 1984: 5. Holotype male, Hungary: Hortobàgy N.P. (HNHM). Paratype examined.

N *illinoiensis* Townsend, 1891: 368. Lectotype male (by designation of O'Hara, 1983a: 307), USA: Illinois (UKL). Lectotype examined.

A *infuscata* (Mesnil), 1952a: 14 (as subspecies of *Crocuta unispina* Mesnil). Holotype male, Zaire: Tshamugussa (MRAC). Holotype examined. New status.

P *ingerae* Andersen, 1982: 161. Holotype male, Denmark: North East Zealand, Bagsvaerd, Smørmose (ZMUC). Holotype examined.

N *intrudens* (Curran), 1932: 14 (*Bucentes*). Holotype male, USA: Pennsylvania, Castle Rock (AMNH). Holotype examined.

U *kairiensis* O'Hara, 1983b: 79. Holotype male, Australia: Queensland, Tinaroo Lake (CAS). Holotype examined.

S *kuscheli* (Cortés), 1952: 110 (*Phantasiosiphona*). Holotype male, Juan Fernandez Islands: Masatierra (CIE). Holotype examined.

A *laticornis* Curran, 1941: 9. Holotype male, South Africa: Pretoria (PPRI). Holotype examined.

A *lindneri* Mesnil, 1959: 22. Holotype male, Tanzania: Msingi (SMNS). Holotype examined.

N,S *longissima* O'Hara, 1983a: 311. Holotype male, Mexico: Chiapas, San Cristobal (CNC). Holotype examined.

N,P *lurida* Reinhard, 1943: 20. Holotype male, USA: Oregon, Rainier (CNC). Holotype examined.

N *lutea* (Townsend), 1919: 584 (*Crocuta*). Lectotype female (by designation of O'Hara, 1983a: 296), USA: New Hampshire, Franconia (USNM). Lectotype examined.

syn. *tenuis* Curran, 1933b: 10. Holotype male, Canada: Ontario, Timagami

(AMNH).— O'Hara, 1983a: 296. Holotype examined.

N *macronyx* O'Hara, 1983a: 313. Holotype male, USA: Washington, Pullman (WSUP). Holotype examined.

P,N *maculata* Staeger *in* Zetterstedt, 1849: 3212. Lectotype male (by designation of Andersen, 1982: 162), Denmark: North East Zealand, Charlottenlund (ZMUC). Lectotype examined.

N *medialis* O'Hara, 1983a: 303. Holotype male, Canada: Nova Scotia, Cranberry Island (CNC). Holotype examined.

A *melania* (Bezzi), 1908: 58 (*Bucentes*). Holotype female, Ethiopia (not located).

A *melanura* Mesnil, 1959: 23. Holotype female, Tanzania: West Kibo (SMNS). Holotype examined.

P *mesnili* Andersen, 1982: 163. Holotype male, Denmark: North East Zealand, Gribskov, Harager Hegn (ZMUC). Holotype examined.

P,N *minuta* (Fabricius), 1805: 282 (*Stomoxys*). Holotype female (head missing), Denmark (ZMUC). Holotype examined.

syn. *analis* Meigen, 1824: 157. Holotype male, Europe (MNHN).— Herting, 1972: 3.

cinerea Meigen, 1824: 156. Holotype female, Europe (MNHN).— Herting, 1972: 4.

cinerea (Latreille), 1809: 338 (*Bucentes*). Type(s), France: Paris (not located).— Herting, 1984: 125.

geniculata (Meigen) of most authors. See *S. geniculata* in list for explanation.

meigenii (Lepeletier and Serville *in* Latreille, et al.), 1828: 501 (*Bucentes*). Replacement name for *S. cinerea* Meigen, 1824 (objective synonym).— Herting, 1984: 125.

nigrovittata Meigen, 1824: 157. Holotype male (MNHN).— Herting, 1972: 11.

tachinaria Meigen, 1824: 156. Holotype male, Federal Republic of Germany: Nordrhein, Aachen (MNHN).— Herting, 1972: 13.

urbanus (Harris), 1780: 153 (*Musca*). Type, England (lost).— Crosskey, 1976b: 100.

N *multifaria* O'Hara, 1983a: 293. Holotype male, Canada: Yukon, Dempster Hwy., mi. 87 (CNC). Holotype examined.

A *munroi* Curran, 1941: 6. Holotype female, South Africa: Fort Jackson (PPRI). Holotype examined.

A *murina* (Mesnil), 1952a: 15 (*Crocuta*). Holotype male, Zaire: Nyongera (MRAC). Holotype examined.

P,N *nigricans* (Villeneuve), 1930: 100 (*Bucentes*). Holotype male, Sweden: Gallivara (CNC). Holotype examined.

syn. *hokkaidensis* Mesnil, 1957: 36. Holotype female, Japan: Hokkaido, Obihiro (CNC).— Herting, 1982: 8. Holotype examined.

martini Andersen, 1982: 169. Holotype male, Sweden: Scania, Hyllstofta (UZI).— Andersen (pers. comm.). Paratype examined.

silvarum Herting, 1967a: 9. Holotype male, Federal Republic of Germany: Freiburg (CNC).— Herting, 1982: 8. Holotype examined.

A *nigrohalterata* Mesnil, 1959: 22 (as ssp. of *S. amplicornis* Mesnil). Holotype male, Tanzania: West Kibo (SMNS). Holotype examined. New status.

A *nigroseta* Curran, 1941: 8. Holotype female, South Africa: Pretoria (PPRI). Holotype examined.

O *nobilis* (Mesnil), 1953: 112 (*Crocuta* (*Siphona*)). Holotype male, Philippines: Mont Palis (ZMU). Holotype examined.

A *obesa* (Mesnil), 1952a: 8 (*Crocuta*). Holotype male, Zaire: Rwindi (MRAC). Holotype examined.

A *obscuripennis* Curran, 1941: 8. Holotype female, Zimbabwe: Vumba Mts. (AMNH). Holotype examined.

N *oligomyia* O'Hara, 1983a: 297. Holotype male, Canada: British Columbia, Keremeos (CNC). Holotype examined.

N *pacifica* O'Hara, 1983a: 291. Holotype male, USA: Washington, Dartford (WSUP). Holotype examined.

P *paludosa* Mesnil, 1960: 188. Holotype male, USSR: Tolmatschevo, Luga (ZIL). Holotype examined.

A *patellipalpis* (Mesnil), 1952a: 10 (*Crocuta*). Holotype male, Zaire: Mt. Sesero (MRAC). Holotype examined.

P *pauciseta* Rondani, 1865: 193. Eight syntypes, Italy (MZF; mixed series according to Herting, 1969a: 198).

- syn. *delicatula* Mesnil, 1960: 190. Holotype male, Great Britain: Chippenham (HDE).— Herting, 1969a: 198. Holotype examined.
- *oculata* Pandellé, 1894: 108.— Lectotype male (by designation of Herting, 1978: 6), France (MNHN).

A *phantasma* (Mesnil), 1952a: 7 (*Crocuta*). Holotype male, Rwanda: Gahinga (MRAC). Holotype examined.

A *pigra* Mesnil, 1977a: 78. Holotype female, Madagascar: Moramanga (MNHN).

N,S *pisinnia* O'Hara, 1983a: 298. Holotype male, USA: New Mexico, 21km. n. Silver City (CNC). Holotype examined.

S *pseudomaculata* Blanchard, 1963: 233. Syntypes, Argentina: Santa Fe (MBR). Syntypes examined.

A *reducta* (Mesnil), 1952a: 18 (*Crocuta*). Holotype male, Zaire: Tshamugussa (MRAC). Holotype examined.

- ssp. *ludicra* Mesnil, 1977a: 78. Holotype male, Madagascar: Manjakatompo (MNHN).

N,S *rizaba* O'Hara, 1983a: 310. Holotype male, Mexico: Veracruz, Orizaba (MSU). Holotype examined.

P *rossica* Mesnil, 1961: 202. Holotype male, USSR: Leningrad, Lugsk (ZIL). Holotype examined.

A *rubrapex* Mesnil, 1977a: 79. Holotype female, Madagascar: Perinet (MNHN).

A *rubrica* (Mesnil), 1952a: 11 (*Crocuta*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined.

A *setinerva* (Mesnil), 1952a: 16 (*Crocuta*). Holotype male, Rwanda: Kibga (MRAC). Holotype examined.

P *setosa* Mesnil, 1960: 191. Holotype male, USSR: Tolmatschevo, Luga (ZIL). Holotype examined.

P *seyrigi* Mesnil, 1960: 189. Holotype male, Canary Islands: Tenerife (MNHN). Holotype examined.

A *simulans* (Mesnil), 1952a: 18 (*Crocuta*). Holotype male, Rwanda: Kundhuru-ya-Tshuve (MRAC). Holotype examined.

A *sola* Mesnil, 1959: 21. Holotype male, Tanzania: Usangi (SMNS). Holotype examined.

A *spinulosa* (Mesnil), 1952a: 12 (*Crocuta*). Holotype male, Zaire: Ngesho (MRAC). Holotype examined.

A *trichaeta* (Mesnil), 1952a: 18 (*Crocuta*). Holotype male, Rwanda: Karisimbi (MRAC). Holotype examined.

N,S *tropica* (Townsend), 1915: 93 (*Phantasiosiphona*). Holotype male, Mexico: Veracruz, San Rafael (USNM). Holotype examined.

A *unispina* (Mesnil), 1952a: 14 (*Crocuta*). Holotype male (abdomen missing), Zaire: Rutshuru (MRAC). Holotype examined.

P *variata* Andersen, 1982: 164. Holotype male, Denmark: Frederikshavn (ZMUC). Holotype examined.

A *vittata* Curran, 1941: 8. Holotype male, Zimbabwe: Salisbury (AMNH). Holotype examined.

A *vixen* Curran, 1941: 9. Holotype female, Zimbabwe: Salisbury (AMNH). Holotype examined.

A *wittei* (Mesnil), 1952a: 5 (*Crocuta*). Holotype male, Rwanda: Karisimbi (MRAC). Holotype examined.

Nomina dubia

P *analis* Robineau-Desvoidy, 1830: 92. Type(s), France (lost).

P *clausa* Robineau-Desvoidy, 1850: 209. Holotype male, France (lost).

P *consimilis* Robineau-Desvoidy, 1850: 205. Holotype male, France (lost).

P *fuscicornis* Robineau-Desvoidy, 1850: 205. Syntypes, France (lost).

P *humeralis* Robineau-Desvoidy, 1850: 207. Syntypes, France (lost).

maculipennis Meigen, 1830: 365. Holotype, Portugal: Algarve (lost).

P *melanocera* Robineau-Desvoidy, 1850: 206. Holotype female, France (lost).

P *pusilla* Robineau-Desvoidy, 1830: 92. Type(s), France: Paris (lost).

syn. *persilla*. Mispelled reference to *pusilla* Robineau-Desvoidy (Coquillett, 1897: 76).

P *quadrinotata* Robineau-Desvoidy, 1850: 203. Holotype female, France (lost).

syn. *quadricincta*. Mispelled reference to *quadrinotata* Robineau-Desvoidy (Rondani, 1859: 10).

P *silvatica* Robineau-Desvoidy, 1850: 208. Holotype male, France (lost).

P *testacea* Robineau-Desvoidy, 1850: 207. Holotype male, France (lost).

P *tristis* Robineau-Desvoidy, 1850: 203. Holotype female, France (lost).

Nomina nuda

S *anthomyformis* Lynch Arribálzaga *in* Brauer, 1898: 505 (13).

P *dorsalis* Brauer and Bergenstamm, 1891: 410.

P *pauciseta* Mesnil, 1964: 856 (as ssp. of *S. geniculata*).

O *taiwanica* (Baranov *in* Hennig), 1941: 195 (*Crocuta*).

4.22 Siphona (Siphonopsis Townsend)

Figs. 18, 24, 30, 97-98, 130, 194-195.

Siphonopsis Townsend, 1916: 622. Type-species, *Siphona plusiae* Coquillett, 1895 (original designation). New status under *Siphona* Meigen.

Recognition

This homogeneous group of three described and approximately 13 undescribed species is New World in distribution, with greatest diversity in the Neotropics.

The male genitalia of *S. (Siphonopsis)* species possess the only states which are unique to this taxon, though the following external characteristics distinguish adults of this taxon from those of most other New World *Siphona s.l.* species: abdomen generally dark in ground color on T_4 and T_5 and medially on T_3, with moderate pruinosity (sparse pruinosity in few species, and resembling abdomen of most *S. (Pseudosiphona)* species); (head of *S. plusiae* shown in Fig. 18) parafacial with several hairs below lowest frontal seta (as in most *Siphona s.l.* species, but different from the more haired parafacial of most *S. (Pseudosiphona)* species); arista almost bare in most species (also in contrast to the haired arista of most *S. (Pseudosiphona)* species); labella of proboscis elongate, varied from two-thirds prementum length to slightly less than prementum length; three postsutural dorsocentral setae; lower katepisternal seta longer than upper anterior one; wing vein R_{4+5} not setulose beyond crossvein *r-m* and CuA_1 bare; and anal vein extended to wing margin.

The most important diagnostic feature of *S. (Siphonopsis)* species externally is labella length. As mentioned above, it varies from two-thirds prementum length to slightly less than prementum length. This feature distinguishes members of this taxon from those of *Siphona s.s.*, in which the labella are at least as long as the prementum. Of several minor external differences between members of *S. (Siphonopsis)* and *S. (Pseudosiphona)* (*cf.* Recognition sections), one of the better is the slightly shorter labella of most (though not all) *S. (Pseudosiphona)* species. Since several other *Siphona s.l.* species have labella as elongate as in *S. (Siphonopsis)* species, it is necessary to examine the male genitalia of *S. (Siphonopsis)*-like specimens for a reliable identification. It is not possible to reliably identify adult females of all New World *Siphona s.l.* species.

Adult males with the above external characteristics are recognized as members of *S. (Siphonopsis)* by the following genitalic states: sternum 5 with apex of apical lobe curved inward; pregonite (Figs. 97-98) slender to average in width, lacking spinules anterolaterally, with (most species) or without (few species) tiny seta posteriorly (medium-sized seta in few species); distiphallus little varied, in profile tapered to narrow truncate tip in most species (Fig. 130), more elongate and lateral apices separated in few species; cerci not sharply inflexed at midpoint. The unique shape of the distiphallus of *S. (Siphonopsis)* species readily separates males with the above external characteristics from males of other *Siphona s.l.* lineages. Most likely to be confused externally with *S. (Siphonopsis)* species are several species of *S. (Pseudosiphona)*, but features of the pregonite, distiphallus and cerci unequivocally separate males of these subgenera. Similarly, the few other *Siphona s.l.* species with *S. (Siphonopsis)*-like labella (see Table 1) differ in male genitalic states (most important of which is distiphallus shape).

Description

Length: 2.5-4.5mm.

Head (Figs. 18, 24, 30).— Proclinate orbital setae subequal in length or anterior one longer. Eye of male medium to medium-large, 0.73-0.84 head height; eye of female subequal to slightly larger than in male. Flagellomere 1 of male short to medium-long, 0.37-0.65 head height; shape from average width to large and triangular. Flagellomere 1 of female smaller than in male in most species, subequal in few. Aristomere 1 short in most species, as long as wide in at least two species. Aristomere two 1.5-6X longer than wide. Aristomere 3 short to long and evenly tapered, almost bare to short plumose. Clypeus narrow and enclosed in membrane. Palpus short, clavate. Proboscis (Figs. 18, 24, 30) with prementum short to medium in length, between 0.6-0.7 head height in most species (not more than about 0.75 head height), labella elongate, 0.7-0.9 prementum length and inflexible in life on about basal third.

Thorax.— Prosternum setulose. Lower katepisternal seta longer than upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.29-0.55 length of proximal portion (mean 0.43). Wing setulae: R_1 dorsally bare, or distally setulose, ventrally bare; R_{4+5} setulose between base and *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent or weakly developed. T_3-T_5 with average setation.

Male genitalia (Figs. 97-98, 130).— S_5 with posterior margins of processes approximately U-shaped; apical lobe large and distinctly differentiated, apex curved inward; median lobe broadly rounded to truncate and relatively unmodified in most species, with accessory lobe slightly to distinctly differentiated in very few species (distinctly differentiated only in *S. conata*); processes moderately setulose. T_6 varied from two lateral sclerites to single dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion 1.0-2.0X width of hypandrial apodeme. Pregonite (Figs. 97-98) in profile curved anteriorly and more or less pointed apically, in few species rather slender (Fig. 98); tiny to medium seta posteriorly in most species, seta absent from at least two species. Epiphallus absent. Distiphallus (Fig. 130) reduced posteriorly, not incised laterally, without enlarged spines anteriorly or laterally, in profile tapered to a narrow truncate tip, in few species distiphallus elongate and very narrow, with apex deeply incised anteriorly and posteriorly (*i.e.* distiphallus with two long arms in posterior view). Postgonite reduced in *S. conata*, short to average length in other species, apically rounded or pointed. Surstylus about average length in most species, elongate in *S. conata*, straight in most species, slightly curved posteriorly in few; basally free from epandrium. Cerci average length in most species, rather short in few, in profile average width to thick; moderately setose on basal half.

Examined male genitalia of: *S. conata*, *S. plusiae*, *S. (Siphonopsis)* spp. A-I,K-N.

Female genitalia.— Short. S_6 with average length hairs. T_6 absent, or present as two tiny to small lateral sclerites or a single median sclerite; spiracles of segment 6 in membrane dorsal to lateral margins of S_6 or in lateral sclerites of T_6. S_7 with long anterior apodeme in most species, short in few; flat and unmodified in most species, in *S. conata* elongate and keeled posteromedially and apically incised. T_7 absent in most species, present as two tiny lateral sclerites in *S. conata*; spiracles of segment 7 in membrane between segments 6 and 7. S_8 distinctly developed, haired. T_{10} present as median sclerite in most species, as two sclerites in very few.

Examined female genitalia of: *S. conata, S. plusiae, S. (Siphonopsis)* spp. A,B,K,M and N.

First instar (Figs. 194-195).— Cephalopharyngeal skeleton: Labrum hatchet-like, though smaller than average in *S. conata* (Fig. 195). Lateral sclerite unmodified. Hypopharyngeal sclerite unmodified. Both dorsal and ventral cornua present.

Posterior abdominal segments of first instar ventrally: Segment 7 with four hooks posteriorly. Segment 8 with one to several uneven rows of small spinules anteriorly; one row of about six to eight spinules posteriorly. Segment 9 bare posteriorly; anus average-sized. Examined first instar of: *S. conata, S. plusiae* and *S. (Siphonopsis)* spp. A,B,K.

Hosts

S. conata and *S. plusiae* attack a serious pest of oak, the California oakworm (*Phryganidia californica*). *S. plusiae* is also recorded from two other insect pests in California, the cabbage looper (*Trichoplusia ni*) and alfalfa looper (*Autographa californica*) (Table 2). Though attacking economically important pest species, *S. conata* and *S. plusiae* do not parasitize their hosts at sufficient densities to be considered good biological control agents.

S. brasiliensis is listed as a parasitoid of two noctuid species in South America (Table 2). However, the name might be a misidentification because *S. (Siphonopsis)* is very diverse in South America and *S. brasiliensis* is the only described species.

Phylogenetics

The distiphallus of males of *S. (Siphonopsis)* species is narrowed to a truncate tip (Fig. 130). The uniqueness of this state within the Siphonini, and its uniformity thoughout the subgenus, provides the best evidence for monophyly of this taxon. A number of other similarities externally and in the male genitalia also suggest that the included species are closely related; however, none can be defended as synapotypic of *S. (Siphonopsis)*. For instance, adults of *S. (Siphonopsis)* species have characteristically elongate labella (Fig. 18), which is shorter (relative to prementum length) than in *Siphona s.s.* species and longer than in most *S. (Pseudosiphona)* species. However, because this state is also present in several other *Siphona s.l.* species belonging to several lineages (see Table 2), it is possible that this state is not independently derived in *S. (Siphonopsis)* but rather synapotypic of this taxon and one of these lineages. Much convergence has occurred among *Siphona s.l.* lineages in the development of elongate labella, so this character can not be used reliably for the grouping of the supraspecific taxa of this genus.

Geographic distribution

Three described and at least 13 undescribed species are included in *S. (Siphonopsis)*. *S. plusiae* is the most widely distributed of the described species, ranging in the west from Oregon to southern Mexico. A closely related, undescribed, species is sympatric with *S. plusiae*, but restricted in known range to California and Arizona. *S. conata* is the only other species of this subgenus known north of Mexico; it is recorded from the San Francisco Bay area, Santa Cruz Island and San Bernardino Mtns. of California.

As in *S. (Pseudosiphona)*, the greatest diversity of *S. (Siphonopsis)* species is in the Neotropics, particularly southern Mexico and southeastern Brazil (the latter area includes the type locality of the only described Neotropical species, *S. brasiliensis*). At least two species range from southern Mexico to southern Brazil. Several species are recognized from western South America from specimens collected in Colombia, Ecuador, Peru, and as far south as central Chile. Specimens have also been collected from Jamaica and Puerto Rico in the Caribbean.

List of described species included in Siphona (Siphonopsis)

S *brasiliensis* Townsend, 1929: 374. Holotype female, Brazil: São Paulo (USNM). Holotype examined.

N *conata* Reinhard, 1959: 162. Holotype male, USA: California, Marin Co., Mill Valley (CAS). Holotype examined.

N *plusiae* (Coquillett), 1895a: 125. (*Siphona*). Lectotype male (by designation of Coquillett, 1897: 76), USA: California (USNM). Lectotype examined.

4.23 Siphona (Uruactia Townsend)

Figs. 68, 99, 131.

Uruactia Townsend, 1927: 256. Type-species, *U. uruhuasi* Townsend, 1927 (original designation). New status under *Siphona* Meigen.

Recognition

This taxon of one described and one undescribed species is only known from three male specimens collected in Ecuador and Peru. Adults are relatively large, 4.0-5.0mm in length, with mostly yellow legs, rather dark thoracic dorsum, wings slightly darkened, abdomen yellow laterally on T_{1+2} and T_3 and rest reddish brown, and sparse abdominal pruinosity. The prementum is about half head height in length, and labella are padlike. These external features help in the recognition of *S. (Uruactia)* species, but examination of the male genitalia is necessary for a positive identification.

The distiphallus of *S. (Uruactia)* species is the most distinctive feature of this taxon. It is smoothly tapered in profile, and with (Fig. 131) or without apical spines. It is similar in appearance to the distiphallus of *S. (Aphantorhapha)* species, but these taxa differ in other genitalic features and externally (*cf.* Recognition sections). Other male genitalic states of *S. (Uruactia)* species include the flattened median lobe of sternum 5 (Fig. 68), bare pregonite (Fig. 99), and inflexed cerci. These states complement the characteristic shape of the distiphallus and help to distinguish members of this taxon from other *Siphona s.l.* species.

The two known species of *S. (Uruactia)* are distinguished from one another by number of postsutural dorsocentral setae, setulation on wing vein R_{4+5}, relative development of lateral marginal setae on abdominal T_{1+2}, and slight differences in male genitalia (as indicated in description below).

Description

Length: 4.0-5.0mm.

Head.— Proclinate orbital setae subequal in length or anterior one longer. Eye of male medium-large, 0.84 head height (same size in all three examined specimens).

Flagellomere 1 of male medium-short to medium, 0.48-0.50 head height; shape average (sp. 31) or broad (*S. uruhuasi*). Aristomere 1 short. Aristomere two 2X longer than wide. Aristomere 3 long and evenly tapered, micropubescent. Clypeus narrow and enclosed in membrane or slightly broadened. Palpus short, clavate. Proboscis with prementum medium in length, slightly longer than half head height, labella padlike.

Thorax.— Prosternum setulose. Lower katepisternal seta longer than upper anterior seta. Three (*S. uruhuasi*) or four (sp. 31) postsutural dorsocentral setae. Upper part of anepisternum with one or two setulae. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.26-0.46 (mean 0.36). Wing setulae: R_1 distally setulose dorsally, ventrally bare; R_{4+5} setulose between base and *r-m* in sp. 31, beyond *r-m* in *S. uruhuasi*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent from *S. uruhuasi*, strong in sp. 31. T_3-T_5 with average setation.

Male genitalia (Figs. 68, 99, 131).— S_5 (Fig. 68) with posterior margins of processes approximately U-shaped; apical lobe distinctly differentiated; median lobe flattened posteromedially, more prominently so in sp. 31 (Fig. 68); processes moderately setulose. T_6 apparently absent. Ejaculatory apodeme with fan-shaped portion subequal in width to width of hypandrial apodeme. Pregonite in profile apically pointed, smoothly curved anteriorly in *S. uruhuasi*, only slightly curved anteriorly in sp. 31 (Fig. 99); bare. Epiphallus absent. Distiphallus reduced posteriorly, entire laterally in *S. uruhuasi*, slightly incised laterally with short posterolateral arm in sp. 31 (Fig. 131), in profile rather narrow and apically pointed, apical margin with small (*S. uruhuasi*) to large (sp. 31) spines. Postgonite average. Surstylus long and straight, basally free from epandrium. Cerci average length, in profile sharply inflexed at midlength; moderately setose on basal half.

Examined male genitalia of: *S. uruhuasi* and sp. 31.

Female genitalia and first instar.— Not examined.

Hosts. Unknown.

Phylogenetics

The two species are interpreted as sister species on the basis of shared states in the male genitalia (particularly shape of median lobes on sternum 5 and shape of distiphallus) and concordant external similarities. This taxon is retained as a subgenus because its sister group within *Siphona s.l.* is unknown.

Geographic distribution

The type species of *S. (Uruactia)* is known only from the male holotype, collected from Uruhuasi, Peru, on 3.II.1910, at an elevation of 1980m, on flowers of *Baccharis* sp. The only other species, sp. 31 (originally numbered in series of unplaced New World *Siphona s.l.*), is represented by two male specimens, one with the same label data as the type of *S. uruhuasi* (USNM) and the other collected from Cerro Tinajillas in the Azuay province of southern Ecuador (18-21.III.1965 at 3100m; CNC).

List of described species included in Siphona (Uruactia)

S *uruhuasi* Townsend, 1927: 364. Holotype male, Peru: Uruhuasi (USNM). Holotype examined.

4.24 New and described New World species unplaced to subgenus in Siphona s.l.

4.24.1 New World Siphona species group 1

Figs. 69, 100-101, 132, 199-201.

This group of approximately nine known species (all undescribed) is Neotropical in distribution, ranging from southern Mexico to southeastern Brazil. They are typical members of the *Siphona* group, with no external autapomorphies. They include spp. 19,21,24-30[3], and are diagnosed as follows (also see Table 1): male eye medium-small to medium-large; male flagellomere 1 medium-short to medium-long, markedly varied in shape from linear or broadened to very broad and subquadrangular or almost triangular; aristomere 1 as long as wide in spp. 26 and 27, short in others; proboscis with labella varied from padlike (few species) to almost length of prementum (most species), flexible in life on apical half or more; three or four postsutural dorsocentral setae; lower katepisternal seta longer than upper anterior seta; postscutellum unusually narrow and projected in spp. 29 and 30; R_1 and R_{4+5} with setulation varied, CuA_1 bare; crossvein *dm-cu* near wing margin in most species, moderately removed from it in few.

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[3] Numbering of species is explained in Methods chapter.

Male genitalia of all nine species examined. S_5 (Fig. 69) with posterior margins of processes approximately U-shaped; apical lobe distinctly differentiated, apex curved inward in few species; median lobe markedly varied from narrow to elongate, rounded to truncate, or rather flattened posteromedially; slightly differentiated accessory lobe in sp. 27, others without. Pregonite (Figs. 100-101) in profile slender to average width, apically rounded to pointed; patch of small spines on apical half or less of sclerotized portion in most species (Fig. 100), spines absent from others (Fig. 101), tiny to moderate-sized seta posteriorly in few species (absent from most). Epiphallus absent. Distiphallus (Fig. 132) relatively distinctive, not incised laterally, without enlarged teeth, in profile nearly parallel-sided on apical half or more and truncate apically. Postgonite markedly reduced in most species, average in few. Surstylus varied from short to long, narrow to broad, straight to curved posteriorly; basally free from epandrium. Cerci thick on apical half in sp. 21, average in others, smoothly curved at midlength.

Female genitalia (examined in spp. 24,27,30) short, unmodified except sternum 8 broader than average in sp. 30.

First instars of three species were examined (spp. 24,27,30; Figs. 199-201). Cephalopharyngeal skeleton with hatchet-like labrum (particularly large in sp. 24, Fig. 199) and otherwise average for *Siphona* group. Species 24 with patch of dense scales externally below hypopharyngeal region. First instar ventrally with two or more large spinules or hooks posteriorly on abdominal segment 7, a row of spinules posteriorly on abdominal segment 8, and abdominal segment 9 bare posteriorly.

Members of *Siphona* species group 1 do not possess any apparent autapomorphies externally. The species grouped together here share similarities in the male genitalia (particularly distiphallus features) that suggest monophyly of the group.

4.24.2 New World Siphona species group 2

Figs. 19, 70, 102-103, 133-134, 202.

This group is comprised of about ten species[4] distributed between southern Arizona and southeastern Brazil. They are typical members of the *Siphona* group, with the following characteristics (also see Table 1): (head of sp. 1 shown in Fig. 19) male eye medium-large to large; male flagellomere 1 medium-short to medium, linear to subquadrangular in shape; aristomere 1 short; proboscis with labella about two-thirds length of prementum in sp. 8, padlike in others; three postsutural dorsocentral setae; lower katepisternal seta longer than upper anterior seta; wing setulation varied; crossvein *dm-cu* slightly removed from wing margin in most species.

Male genitalia of all ten included species examined. S_5 (Fig. 70) with posterior margins of processes approximately U-shaped; apical lobe distinctly differentiated, apex curved inward in few species; median lobe markedly varied from broadly rounded to elongate and truncate or flattened posteromedially, accessory lobe distinctly differentiated in few species. Pregonite (Figs. 102-103) varied in profile, smoothly to sharply curved anteriorly, average to broad on basal half; with or without patch of small spines on apical half or less of sclerotized portion and in sp. 2 (Fig. 103) with longitudinal row of spines, bare posteriorly or with tiny to moderate-sized seta. Epiphallus absent. Most included species are recognized as members of this species group by features of the distiphallus: most possess posterolaterally on each side a ventrally or anteroventrally directed projection or hook (Figs. 133-134); a few species lack this feature of the distiphallus but are included in this species group (with varied degrees of confidence) because of other external and genitalic similarities; posterior margin of distiphallus entire in sp. 2, incised in others. Postgonite markedly reduced in spp. 3 and 10, short in sp. 2, average in others. Surstylus average length to elongate, straight to curved posteriorly; basally free from epandrium. Cerci rather short to average length, straight to smoothly curved.

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[4] These species are numbered from one to ten, separately from those of species groups 1 and 3 and unplaced New World species, as explained in Methods chapter.

Female genitalia (examined in spp. 3 and 6) short, unmodified except sternum 8 broader than average.

The first instar of sp. 3 (Fig. 202) is typical of the *Siphona* group, with a hatchet-like labrum, distinct cornua and four ventral hooks posteriorly on segment 7.

The conservative external features of members of *Siphona* species group 2 make this group difficult to recognize. In addition certain species are less apomorphic than most in their male genitalic features, so their inclusion here is tentative and is based on general similarities.

4.24.3 New World Siphona species group 3

Figs. 104-105, 135, 203.

Five undescribed New World species are recognized as belonging to a monophyletic lineage possibly related to *Siphona* species group 1 (see below). Included are sp. 3 (ranging from Washington state to southern California and Arizona), sp. 4 (Veracruz and Chiapas, Mexico), sp. 6 (Florida, ?Chiapas), sp. 12 (Iowa, Ohio and Ontario) and sp. 22 (SE Brazil)[5]. Externally these flies are quite varied, particularly in head features and wing setulation, and for this reason specimens of some of these species appear more externally similar to excluded species than to their own group members. As a rule, male genitalic characteristics are more reliable indicators of relationship within *Siphona s.l.* than are external features (species of *S. (Pseudosiphona)* and *S. (Siphonopsis)* being good examples), so little weight is given here to such homoplastic external similarities.

Siphona species group 3 is diagnosed as follows (also see Table 1): male eye medium to medium-large; male flagellomere 1 markedly varied, medium-short to long; shape linear to very broadly triangular; proboscis with labella slightly lengthened in some specimens of sp. 22, padlike in others; three postsutural dorsocentral setae; varied wing setulation; position of

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[5] Numbering of these species is explained in Methods chapter.

crossvein *dm-cu* varied; legs and abdomen average; (male genitalia examined in all five species) sternum 5 with posterior margins of processes approximately U-shaped, apical lobe not apically curved inward, median lobe rounded to elongate and truncate, distinctly differentiated accessory lobes in sp. 4; pregonite (Figs. 104-105) in profile rather sharply curved at midlength or smoothly curved anteriorly, with longitudinal ridge of spines laterally (resembling pregonite of *Entomophaga* and *Proceromyia* except possessing tiny to moderate-sized seta posteriorly in most specimens [*i.e.* of two examined specimens of sp. 22, one has tiny seta and the other is bare, Fig. 105] - this seta only present among *Siphona* group taxa); epiphallus absent; distiphallus (Fig. 135) not incised laterally, characteristically squared-off basally, with short, parallel-sided apical portion ending in truncate tip, moderately developed spines anteriorly in sp. 22, only spinules present in others; postgonite average to reduced; surstylus and cerci average; female genitalia short and unmodified (examined only in sp. 3); first instar (examined only in sp. 3, Fig. 203) with hatchet-like labrum, four ventral hooks posteriorly on abdominal segment 7, and other characteristics typical of *Siphona* group taxa.

Two members of *Siphona* species group 1 (spp. 26 and 27) have similar distiphallus structure to species of group 3, but differ in features of the pregonite. Species of group 3 possess a spined longitudinal ridge on the outer surface of the pregonite, a state not found in other species of *Siphona s.l.* except in *Siphona* sp. grp. 2, sp. 2 (Fig. 103). (Members of group 3 also lack small spines apically on the pregonite, a state found in spp. 26 and 27, but since this state is found elsewhere among certain lineages of New World *Siphona s.l.* it is probably plesiomorphic at this level of interpretation.) There are both external similarities and dissimilarities between members of both groups 1 and 3, but these involve such homoplastic characters that their phylogenetic interpretation is difficult. I have not studied the groups in sufficient detail to offer any definite views about the possible interrelationships of groups 1 and 3, but I suggest that certain male genitalic similarities may indicate that the species of group 3 are derived members of group 1 or the groups are sister groups.

I have presented the information above about *Siphona* group 3, as I have elsewhere for groups 1 and 2, to provide a tentative framework upon which a formal taxonomic investigation of the numerous undescribed and unplaced New World *Siphona s.l.* species can be built. These notes about undescribed New World siphonines ought to prove useful in the eventual revision of this large and unworked assemblage of *Siphona* species.

4.24.4 Unplaced New World species of Siphona

Figs. 20, 106, 136, 204-209.

I have left two described species unplaced within New World *Siphona s.l.*: *Siphona panamensis* (Curran) and *Siphona pulla* (Reinhard). Though typical members of *Siphona s.l.*, these species cannot be associated with any of the subgenera here recognized nor the three additional species groups discussed. Both are difficult to place because they are only known from female holotypes, and if males were available then unequivical placement of these species might be possible.

Specimens of many undescribed species were examined during the course of this revision. Those belonging to relatively easily recognized genera are incorporated into the descriptions of those genera and not themselves described or specially treated. This practise is more difficult within *Siphona s.l.* because monophyletic lineages are difficult to recognize and many species cannot be associated with the lineages that are. The complexity is all the more difficult to discuss since most of the species are undescribed. As this is primarily a generic level revision it is impractical at this time to describe these new species, though discussing them in an informal manner will convey some idea of their diversity. Where possible descriptions of certain subgenera (particularly *S. (Pseudosiphona)* and *S. (Siphonopsis)*) have been modified for inclusion of appropriate undescribed species, but even though this has been done and *Siphona* groups 1 to 3 informally diagnosed, at least 15 undescribed New World species remain that I have studied but not been able to place. I intend below to outline some of the diversity contained within this group of mostly unrelated species because they may remain undescribed for some time. As new groups or subgenera are erected for some of these species and other species identified as related to groups recognized here, the descriptions of the latter will have to be modified for such inclusions. For the present I have retained a rather conservative approach toward recognition of New World *Siphona* subgenera in order to keep them as monophyletic lineages (and thus, I believe, more meaningful entities) in the midst of a plethora of undescribed forms.

The species discussed here include *S. panamensis*, *S. pulla*, and 15 numbered species: spp. 1,2,5,7,8,10,13-17,20,23,32 and 34[4]. Their range of variation is given in Table 1 under the heading of "*Siphona s.l.*, unplaced", and the assemblage is briefly diagnosed here: (head of sp. 23 shown in Fig. 20) male eye medium-small to very large; male flagellomere 1 short to medium, shape linear, broadened, subquadrangular or broad and triangular; proboscis with labella padlike in most species, slightly lengthened in few, about as long as prementum in spp. 13 and 23 (Fig. 20); three postsutural dorsocentral setae in most species, four in few; lower katepisternal seta longer than upper anterior seta in most species, subequal in length in few, shorter in spp. 14 and 17; R_1 and R_{4+5} with setulation varied, CuA_1 bare; crossvein *dm-cu* positioned near or removed from wing margin; legs average.

Male genitalia of 14 species examined (spp. 1-2,5,7-8,10,13-17,23,32,34). S_5 with posterior margins of processes approximately U-shaped in most species, obtusely angled in few, nearly V-shaped in spp. 7 and 15 (though median cleft more distinct than in *Actia* species); apical lobe distinctly differentiated, apex curved inward in some species; median lobe varied, rounded, elongate, truncate, or slightly flattened posteromedially, accessory lobe present in sp. 5; pregonite (Fig. 106) varied, in profile slender to broad, apically pointed to rounded, small spines on sclerotized portion apically in few species, with tiny to moderate-sized seta posteriorly in most species, seta absent from few. Epiphallus absent. Distiphallus (Fig. 136) markedly varied, laterally incised or complete, with or without enlarged spines apically, in profile varied apically from pointed or rounded to truncate. Postgonite average in most species, reduced in spp. 32 and 34. Surstylus and cerci average in most species, surstylus basally free from epandrium.

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[4] Numbering of these species is explained in Methods chapter.

Female genitalia examined in seven species (spp. 1-2,5,10,14,20,23), short; S_6 sharply keeled posteromedially in sp. 20, flat in others; T_6 absent, or present as lateral sclerites or (in sp. 3) as a dorsally continuous sclerite; S_7 with rather short anterior apodeme in sp. 20, long in others, sharply keeled posteromedially only in sp. 20; S_8 average in most species, very broad in sp. 5, with thick setae in sp. 20.

First instars of six species examined (spp. 1-2,10,14,20,23; Figs. 204-209). Cephalopharyngeal skeleton with hatchet-like labrum, which has a pronounced ventral projection in sp. 10 (Fig. 206), and is curved downward and unusually arched dorsally in sp. 20; cornua present, though dorsal cornu of varied length; first instar of sp. 20 with dense patch of scales ventrally below cephalopharyngeal skeleton. Posterior abdominal segments of first instar ventrally: four hooks posteriorly on segment 7 in most species, with row of large spinules in spp. 1 (Fig. 204), 10 (Fig. 206) and 23; segment 8 posteriorly with row of spinules; segment 9 bare posteriorly.

This group of species is, by definition, restricted to the New World. The highest concentration of species (six) is in southern Mexico, with seven other species distributed throughout North America from Alaska to northcentral Mexico and four species distributed between southeastern Brazil and lower Central America.

Hosts are known only for New World species 7 and 8, and include larvae of several species of the Geometridae and one of the Noctuidae. Species 7 and 8 are recorded from southern British Columbia, Canada.

List of described species unplaced to subgenus in New World *Siphona*

S *Actia panamensis* Curran, 1933a: 3. Holotype female, Panama: Barro Colorado Is. (AMNH). Holotype examined. (Removed from *Actia*.)

N,S *Aphantorhapha pulla* Reinhard, 1974: 1157. Holotype female, Mexico: Morelos, Cuernavaca (CNC). Holotype examined. (Removed from *Aphantorhapha*.)

4.25 *Actia heterochaeta* Bezzi, unplaced species of Siphonini

I have been unable to locate the female type of this species, described from Ethiopia by Bezzi (1908: 59). The type apparently does not reside in Milan (MCSN) with many of the other Bezzi types (Arnaud 1982).

Actia heterochaeta was described by Bezzi under a concept of *Actia* now equivalent to the entire Siphonini. The original description fails to mention a single generic characteristic that would help in the placement of this species. Bezzi compares *A. heterochaeta* with *A. bicolor* (now in *Ceromya*) in his original description, and then with *A. stiglinae* (now in *Peribaea*) in a later publication (1928: 204). It is clear that Bezzi's concept of "allied species" was based on shared similarities and not commonality of descent, so his species comparisons provide no clue about the correct placement of *A. heterochaeta*.

I examined a male specimen in the BMNH collected from Nigeria and identified by Villeneuve as *A. heterochaeta*. This specimen is probably the one mentioned by Crosskey (1980: 855) as a questionable new locality record for the species. However, Villeneuve's identification is probably in error because the specimen differs from the description of *A. heterochaeta* in two important respects: R_1 is bare in *A. heterochaeta* and distally setulose in Villeneuve's specimen, and coloration differs markedly (even given that Bezzi's specimen was a female and Villeneuve's specimen a male). Without any concrete indication of the generic characteristics of *A. heterochaeta*, I must leave this species unplaced in the Siphonini, as did Crosskey (1980: 855).

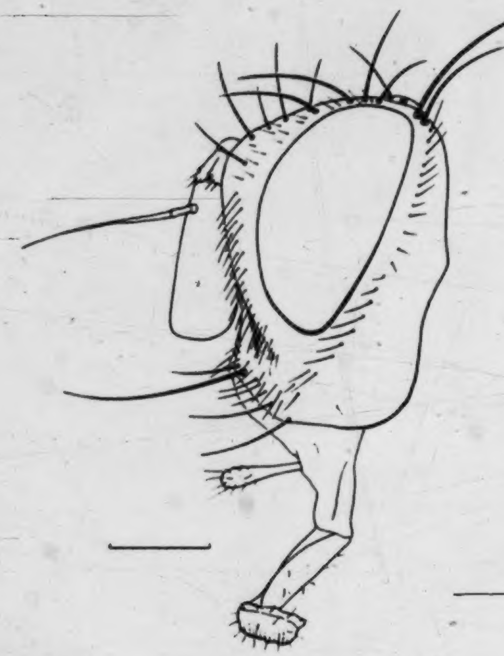
Figures 1 to 4. Head profiles of male siphonines (vestiture of postcranium omitted). Scale bars = 0.5mm.

Figure 1. *Goniocera io*.

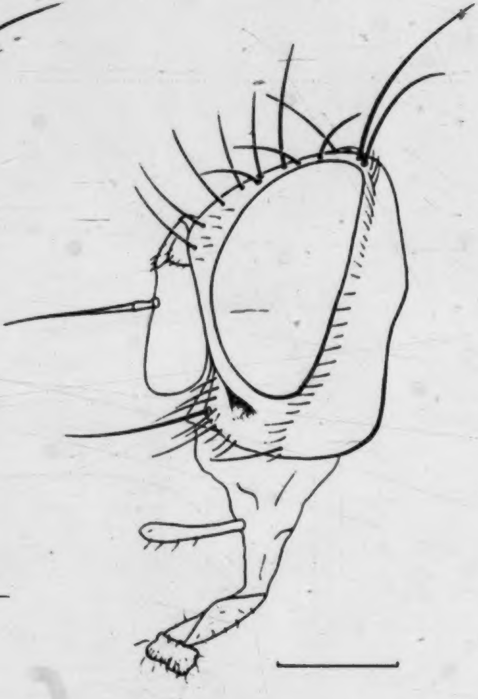
Figure 2. *Proceromyia macronychia*.

Figure 3. *Proceromyia pubioculata* (eye densely haired).

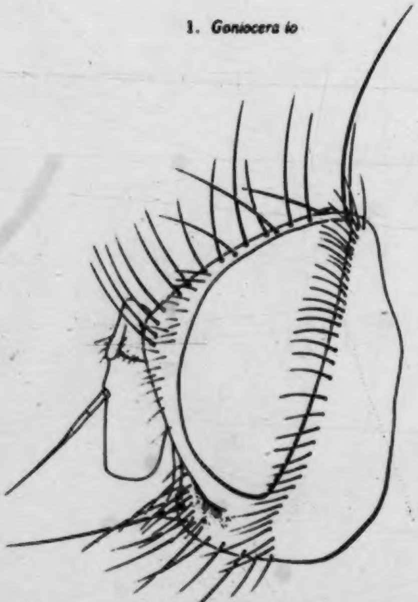
Figure 4. *Entomophaga exoleta*.



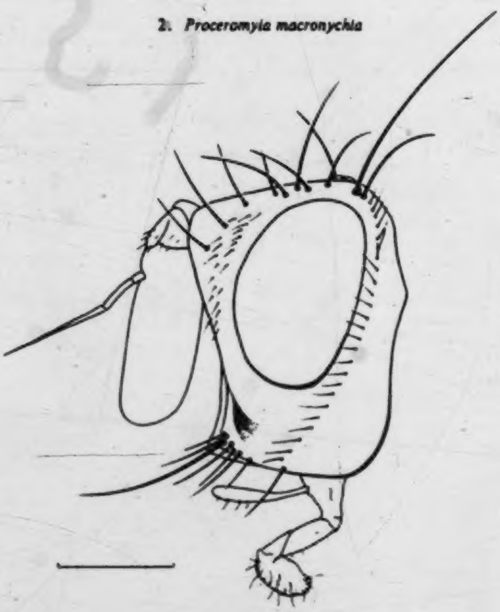
1. *Goniocera io*



2. *Proceromyia macronychia*



3. *Proceromyia pubioculata*



4. *Entomophaga exoleta*

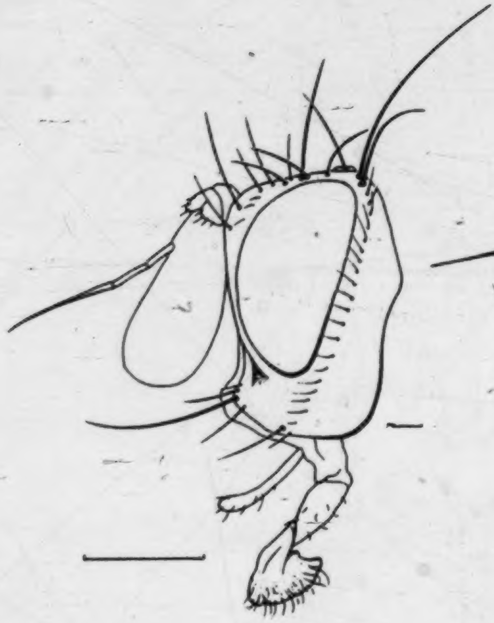
Figures 5 to 8. Head profiles of male siphonines (vestiture of postcranium omitted). Scale bars = 0.5mm.

Figure 5. *Entomophaga nigrohalterata*.

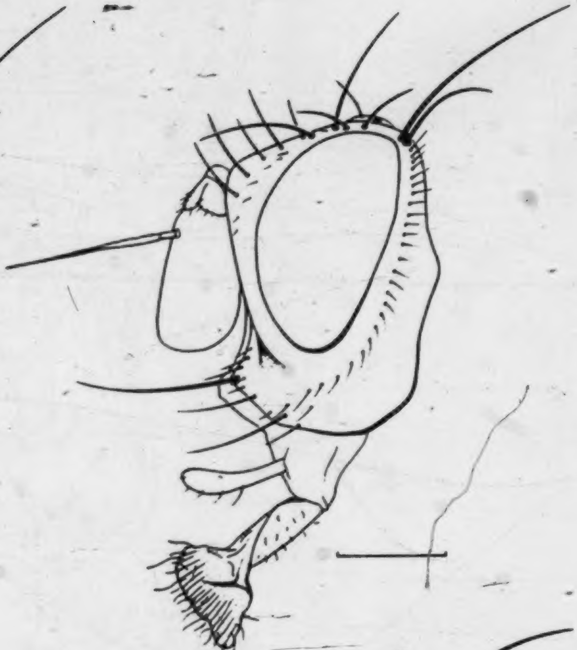
Figure 6. *Ceromya flaviceps*.

Figure 7. *Ceromya* New Guinea sp. 15.

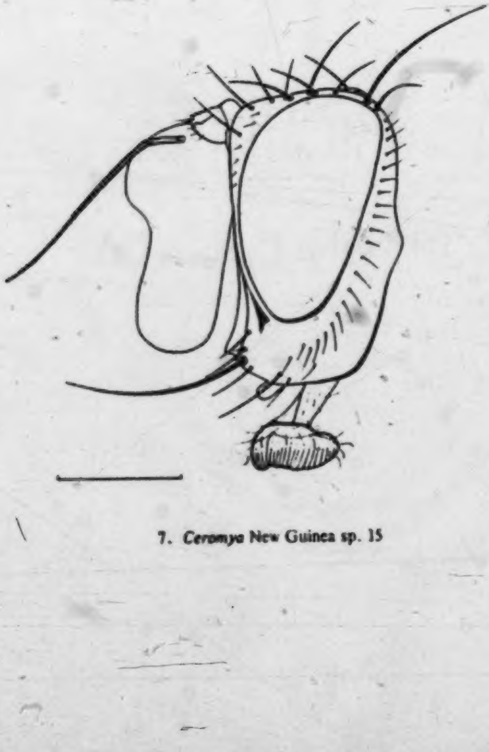
Figure 8. *Actia lamia*.



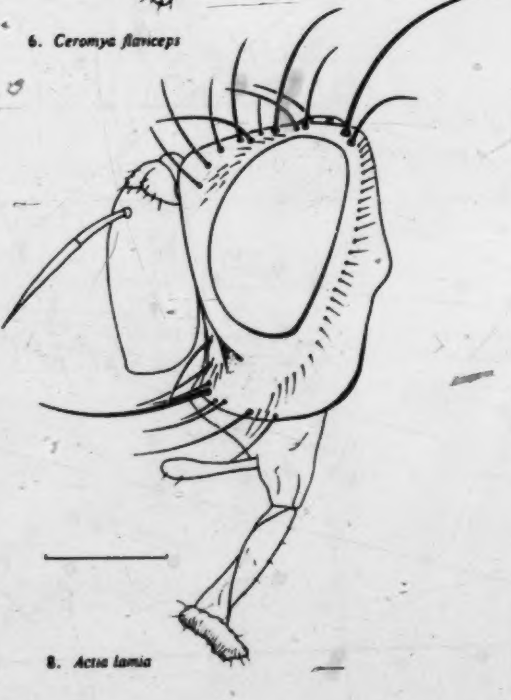
5. *Entomophaga nigrohalterata*



6. *Ceromya flaviceps*



7. *Ceromya* New Guinea sp. 15



8. *Actia lamia*

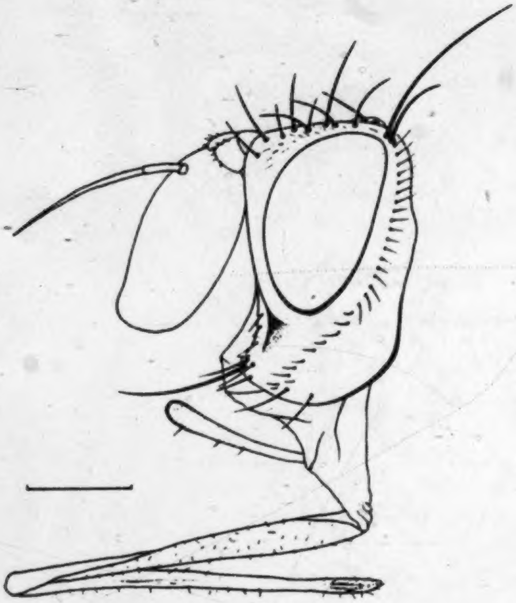
Figures 9 to 12. Head profiles of male siphonines (vestiture of postcranium omitted). Scale bars = 0.5mm.

Figure 9. *Actia* Nepal sp. 1.

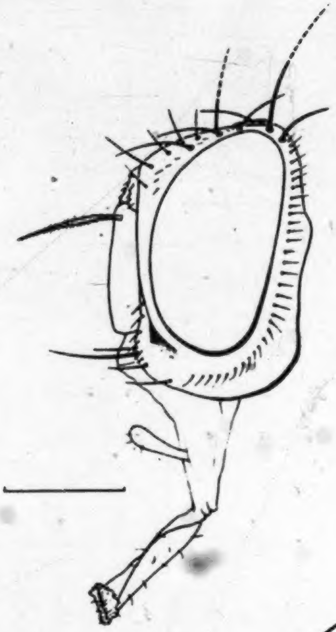
Figure 10. *Actia parviseta* (from holotype, proboscis reoriented).

Figure 11. *Peribaea cervina* (from holotype, vibrissae missing).

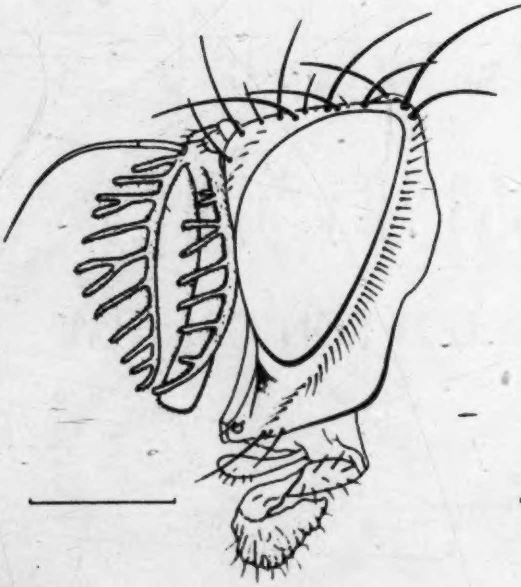
Figure 12. *Peribaea tibialis*.



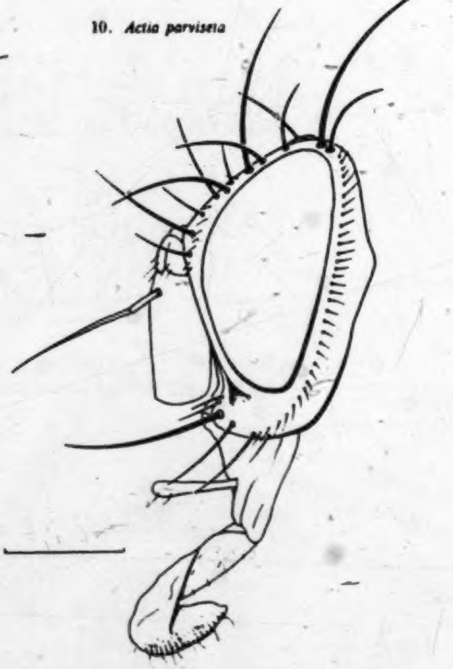
9. *Actia* Nepal sp. 1



10. *Actia parviseta*



11. *Peribaea cervina*



12. *Peribaea tibialis*

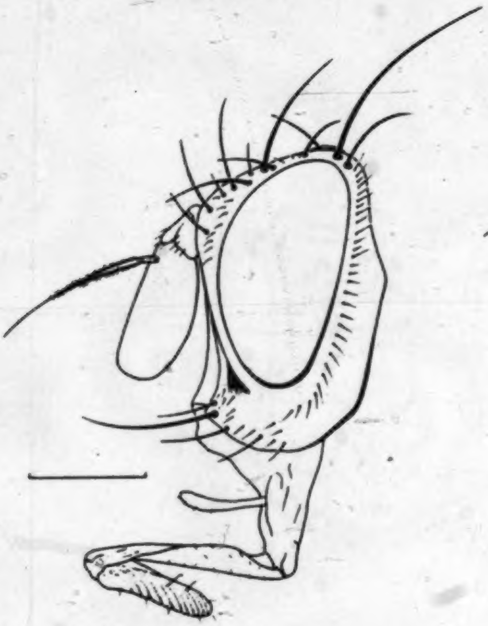
Figures 13 to 16. Head profiles of male siphonines (vestiture of postcranium omitted). Scale bars = 0.5mm.

Figure 13. *Siphona (Actinocrocuta) singularis* complex.

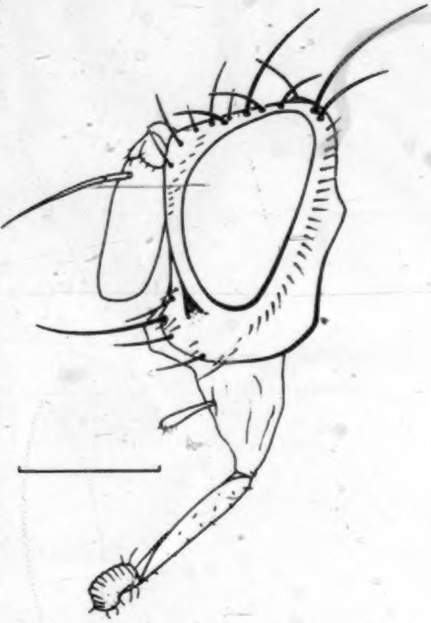
Figure 14. *Siphona (Aphantorhapha) arizonica.*

Figure 15. *Siphona (Baeomyia) xanthogaster* (from holotype).

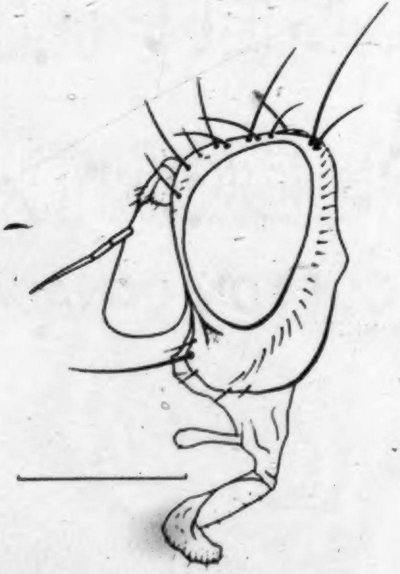
Figure 16. *Siphona (Ceranthia) flavipes.*



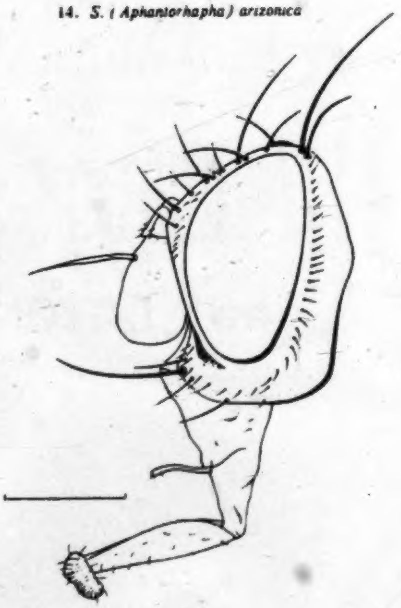
13. *S.* (*Actinocrocuta*) *singularis* complex



14. *S.* (*Aphantorhapha*) *arizonica*



15. *S.* (*Baeomyia*) *xanthogaster*



16. *S.* (*Ceranthia*) *flavipes*

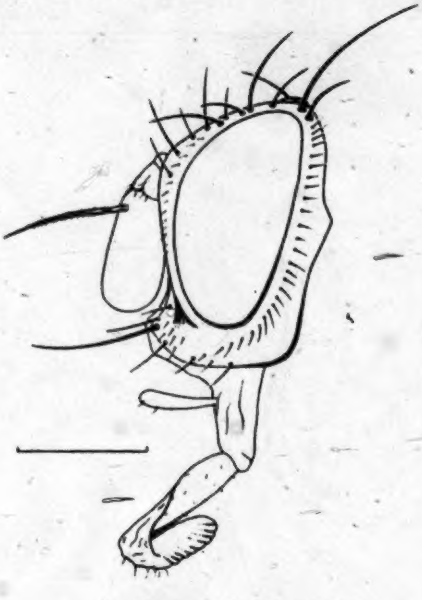
Figures 17 to 20. Head profiles of male siphonines (vestiture of postcranium omitted). Scale bars = 0.5mm.

Figure 17. *Siphona (Pseudosiphona) brevirostris.*

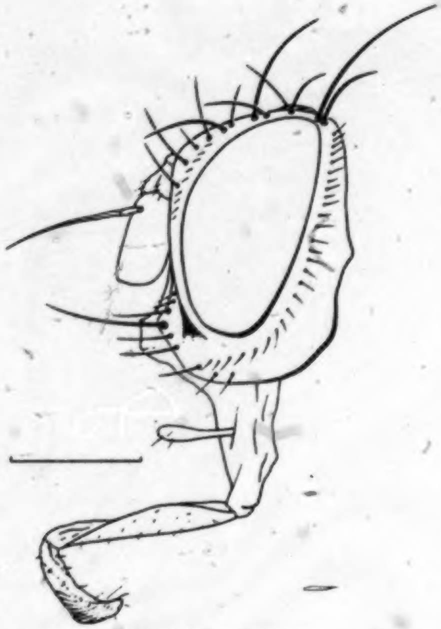
Figure 18. *Siphona (Siphonopsis) plusiae.*

Figure 19. *Siphona s.l.*, sp. grp. 2, sp. 1.

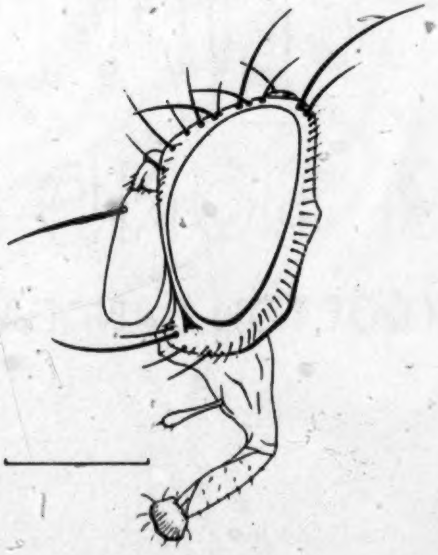
Figure 20. *Siphona s.l.*, unplaced sp. 23.



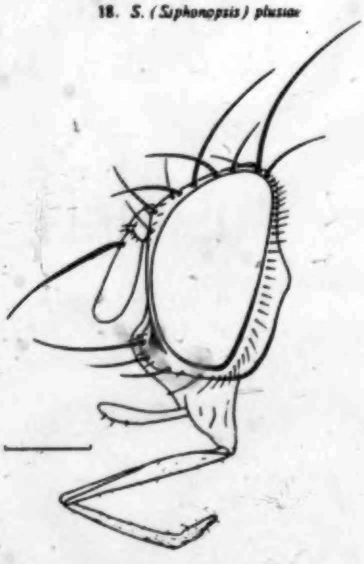
17. *S. (Pseudosiphona) brevirostris*



18. *S. (Siphonopsis) plusiae*



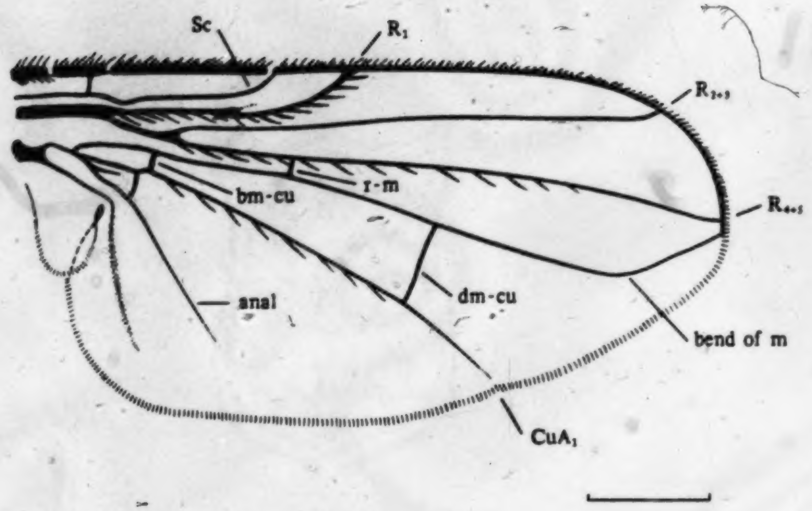
19. *Siphona s.l.*, sp. grp. 2, sp. 1



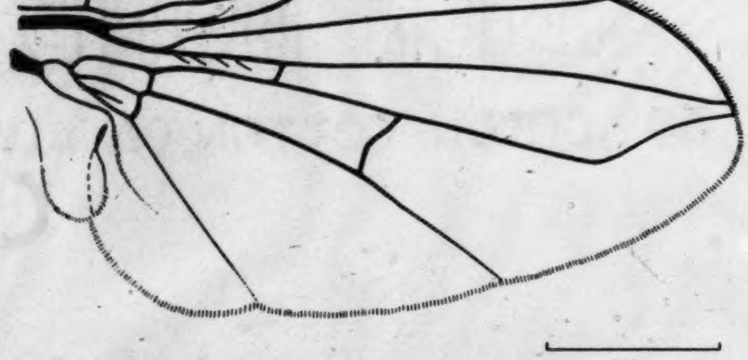
20. *Siphona s.l.*, unplaced sp. 23

Figure 21. Wing of *Actia interrupta*, with wing veins labelled. Scale bar = 0.5mm.

Figure 22. Wing of *Siphona (Baeomyia) xanthogaster*. Scale bar = 0.5mm.


Sc
R_1
R_{2+3}
r-m
bm-cu
R_{4+5}
anal
dm-cu
bend of m
CuA_1

21. *Actia interrupta*



22. *S. (Baeomyia) xanthogaster*

Figures 23 to 26. Comparison of proboscis structure. Scale bars = 200μm.

Figure 23. *Actia diffidens*, with padlike labella.

Figure 24. *Siphona (Siphonopsis) plusiac*, with elongate labella.

Figure 25. *Siphona (Siphona) maculata*, with long labella.

Figure 26. *Siphona (Siphona) pisinnia*, with very long labella (*lbl*, labella; *prem*, prementum).

Figures 27 to 28. Left lateral view of prothorax, for comparison of proepimeral setae. Scale bars = 100μm.

Figure 27. *Peribaea* sp., illustrating two strong and opposed proepimeral setae (*a spr*, anterior spiracle; *l prepm s*, lower proepimeral seta; *u prepm s*, upper proepimeral seta).

Figure 28. *Siphona (Siphona) maculata*, illustrating single strong proepimeral seta (upper and lower setae indicated by arrows).

Figures 29 to 30. Comparison of labella of proboscis. Scale bars = 100μm.

Figure 29. Labella of *Actia diffidens*, illustrating padlike condition and numerous pseudotracheae.

Figure 30. Labella of *Siphona (Siphonopsis) plusiae*, illustrating elongate condition and relatively few pseudotracheae.

23

24

25

26

27

28

29

30

Figures 31 to 32. Left lateral view of thorax, for comparison of katepisternal and anepisternal setae. Scale bars = 250μm.

Figure 31. ***Actia diffidens*****,** illustrating short lower katepisternal seta (***l kepst s***) and two anepisternal setulae (***anepst s***).

Figure 32. ***Siphona (Siphona) maculata*****,** illustrating long lower katepisternal seta and single anepisternal setula (indicated by arrows).

Figures 33 to 34. Ventral view of mesothorax, for comparison of posteroventral region of katepisternum. Scale bars = 200μm.

Figure 33. ***Actia diffidens*****,** illustrating row of hairs on katepisternum (***kepst h***) anterior to mid coxa.

Figure 34. ***Siphona (Siphona) maculata*****,** illustrating presence of several hairs on katepisternum restricted to midline region (indicated by arrow).

Figures 35 to 36. Comparison of anterior surface of mid femur. Scale bars = 200μm.

Figure 35. ***Ceromya varichaeta*****,** illustrating patch of tiny hairs on anterior surface of mid femur (***fem h***).

Figure 36. ***Siphona (Siphona) maculata*****,** illustrating typical condition of anterior surface of mid femur.

Figures 37 to 38. Comparison of anterior surface of mid tibia. Scale bars = 200μm.

Figure 37. ***Ceromya varichaeta*****,** illustrating presence of strong anterodorsal seta (***ad s***) on mid tibia.

Figure 38. ***Siphona (Baeomyia) xanthogaster*****,** illustrating absence of anterodorsal seta on mid tibia.

anepst s
l kepst s

31

32

33

34

35

36

37

38

Figures 39 to 42. Comparison of male pregonite structure. Scale bars = $40\mu m$.

Figure 39. Left lateral view of pregonite of *Ceromya americana* complex, illustrating spinules on membranous portion (*memb p*, membranous portion; *scl p*, sclerotized portion; *spin*, spinules).

Figure 40. Ventrolateral view of pregonite of *Ceromya americana* complex.

Figure 41. Left lateral view of pregonite of *Actia diffidens*, illustrating large spines (*sp*) on sclerotized portion.

Figure 42. Ventral view of pregonite of *Actia diffidens*.

Figures 43 to 46. Comparison of female genitalia. Scale bars = $100\mu m$.

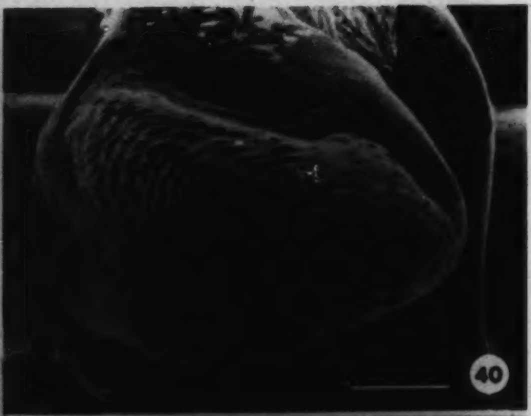
Figure 43. Ventral view of female genitalia of *Siphona (Siphona) maculata*, illustrating unmodified sterna (sterna numbered; *cer*, cercus).

Figure 44. Ventral view of female genitalia of *Siphona (Ceranthia) flavipes*, illustrating keel (*kl*) posteromedially on sternum 7.

Figure 45. Lateral view of female genitalia of *Siphona (Siphona) maculata*.

Figure 46. Lateral view of female genitalia of *Siphona (Ceranthia) flavipes*.

scl p
memb p
spin
39


40

memb p
scl p
sp
41

42

5
6
7
8
10
cer
43

kl
44

45

46

Figures 47 to 58. Ventral view of male sternum 5. Scale bars = 0.1mm.

Figure 47. *Goniocera schistacea* (Y68, CNC) (***ap l***, apical lobe; ***bs p***, basal plate; ***descl a***, desclerotized area; ***med c***, median cleft; ***med l***, median lobe).

Figure 48. *Proceromyia macronychia* (Y40, CNC).

Figure 49. *Proceromyia pubioculata* (Y85, JEOH).

Figure 50. *Entomophaga exoleta* (Y132, ZMUC).

Figure 51. *Entomophaga nigrohalterata* (Y27, CNC).

Figure 52. *Ceromya silacea* (Y179, CNC).

Figure 53. *Ceromya flaviceps* (Y107, CNC).

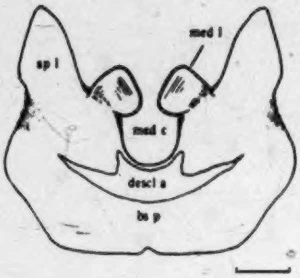
Figure 54. *Ceromya* New Guinea sp. 18 (Y175, BLKU).

Figure 55. *Ceromya americana* complex (Y26, CNC).

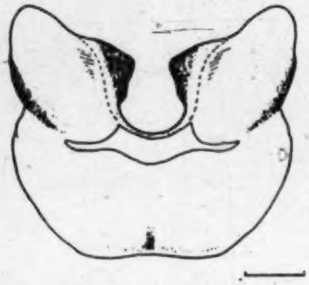
Figure 56. *Ceromya amblycera* (Y45, UCS).

Figure 57. *Ceromya lutea* (Y121, CNC).

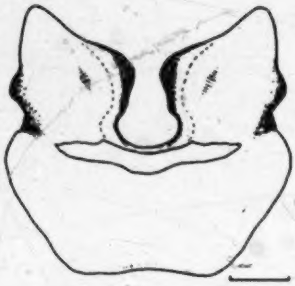
Figure 58. *Actia lamia* (Y17, JEOH).



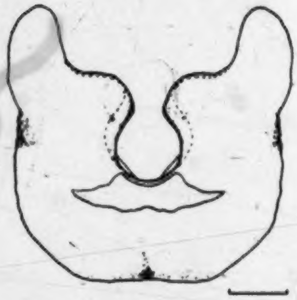
47. *Goniocera schistacea*



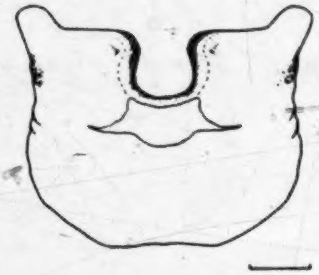
48. *Proceromyia macronychia*



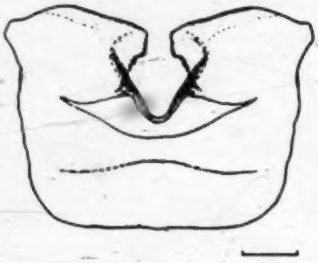
49. *Proceromyia pubioculata*



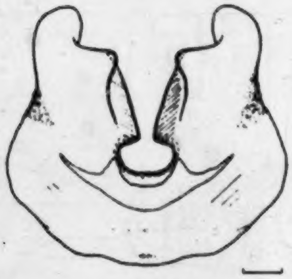
50. *Entomophaga exoleta*



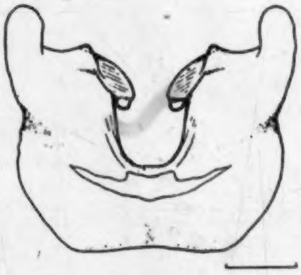
51. *Entomophaga nigrohalterata*



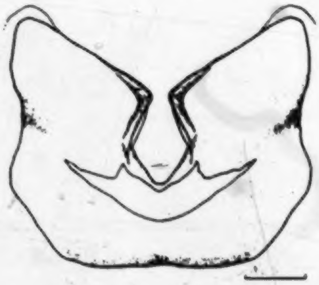
52. *Ceromya silacea*



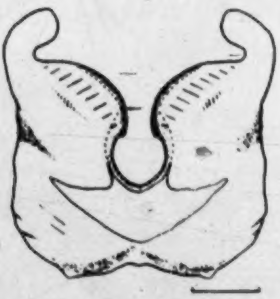
53. *Ceromya flaviceps*



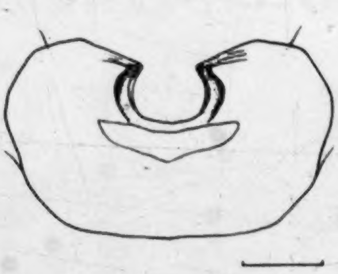
54. *Ceromya* New Guinea sp. 18



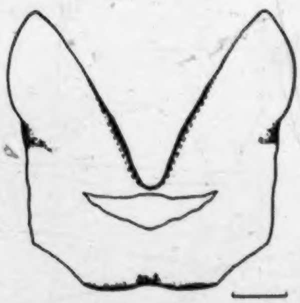
55. *Ceromya americana* complex



56. *Ceromya amblycera*



57. *Ceromya lutea*



58. *Actia lamia*

Figures 59 to 70. Ventral view of male sternum 5. Scale bars = 0.1mm.

Figure 59. *Actia autumnalis* (Y22, CNC).

Figure 60. *Peribaea apicalis* (Y82, CNC).

Figure 61. *Peribaea* Australia sp. 1 (Y83, DPI).

Figure 62. *Siphona (Actinocrocuta) singularis* complex (O120, CNC).

Figure 63. *Siphona (Aphantorhapha) arizonica* (unnumbered, JEOH).

Figure 64. *Siphona (Aphantorhaphopsis)* Nepal sp. 1 (W75, CNC).

Figure 65. *Siphona (Ceranthia) flavipes* (B8, CNC).

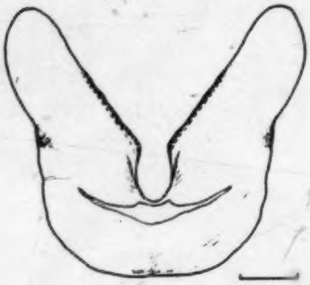
Figure 66. *Siphona (Pseudosiphona)* sp. 4 (R22, CNC).

Figure 67. *Siphona (Siphona) geniculata* (W38, JEOH).

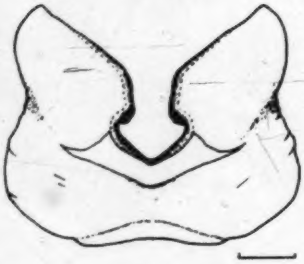
Figure 68. *Siphona (Uruactia)* sp. 31 (R45, CNC).

Figure 69. *Siphona s.l.*, sp. grp. 1, sp. 28 (O27, CNC).

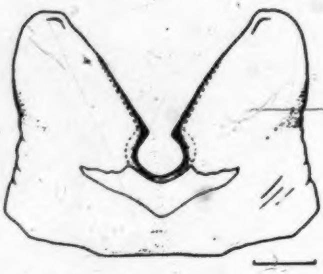
Figure 70. *Siphona s.l.*, sp. grp. 2, sp. 9 (O154, USNM).



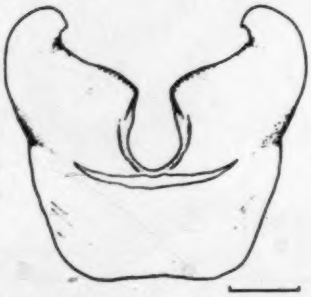
59. *Actia autumnalis*



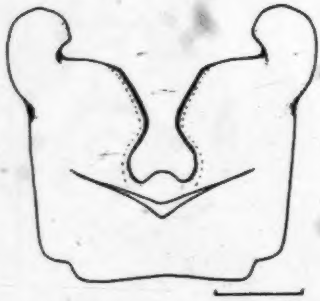
60. *Peribaea apicalis*



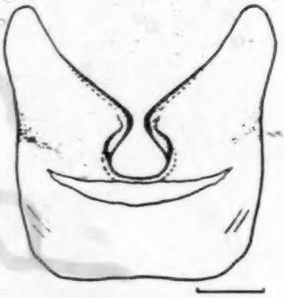
61. *Peribaea* Australia sp. 1



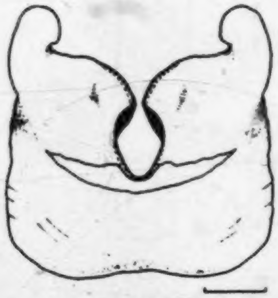
62. *S.* (*Actinocrocuta*) *singularis* complex



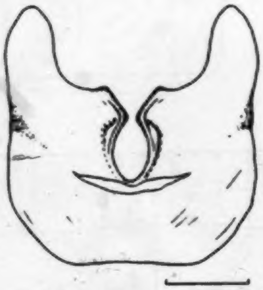
63. *S.* (*Aphantorhapha*) *arizonica*



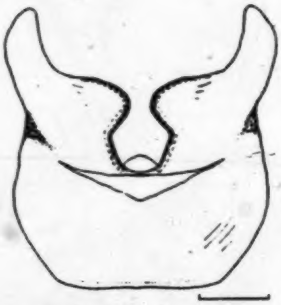
64. *S.* (*Aphantorhaphopsis*) Nepal sp. 1



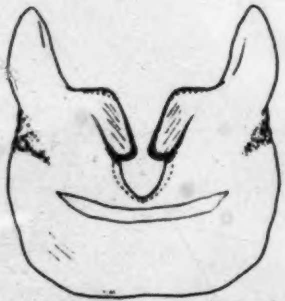
65. *S.* (*Ceranthia*) *flavipes*



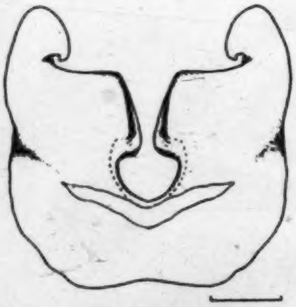
66. *S.* (*Pseudosiphona*) sp. 4



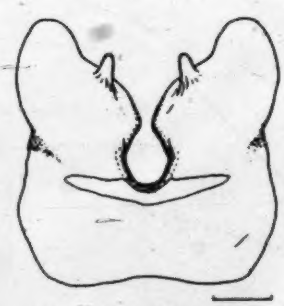
67. *S.* (*Siphona*) *geniculata*



68. *S.* (*Uruactia*) sp. 31



69. *Siphona s.l.*, sp. grp. 1, sp. 28



70. *Siphona s.l.*, sp. grp. 2, sp. 9

Figures 71 to 79. Lateral view of male pregonite. Scale bars = 0.05mm.

Figure 71. *Goniocera io* (Y41, CNC).

Figure 72. *Goniocera versicolor* (Y69, CNC).

Figure 73. *Proceromyia macronychia* (Y40, CNC).

Figure 74. *Proceromyia pubioculata* (Y85, JEOH).

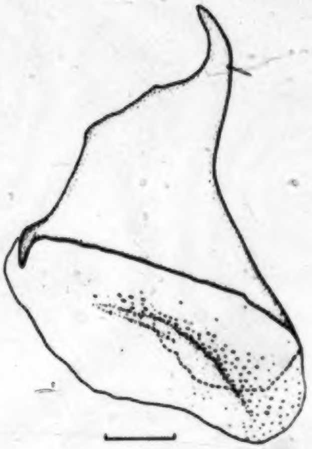
Figure 75. *Entomophaga exoleta* (Y132, ZMUC).

Figure 76. *Entomophaga nigrohalterata* (Y27, CNC).

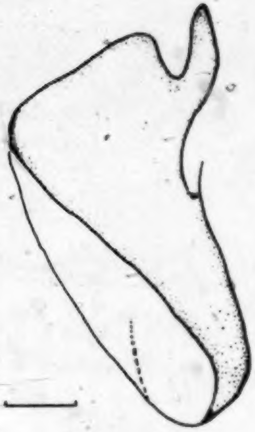
Figure 77. *Ceromya flaviceps* (Y107, CNC).

Figure 78. *Ceromya* New Guinea sp. 6 (Y176, BLKU).

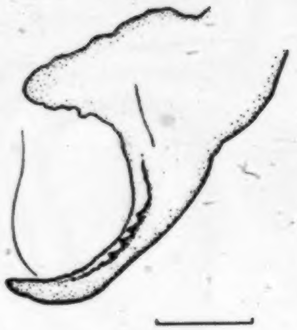
Figure 79. *Ceromya americana* complex (Y25, CNC).



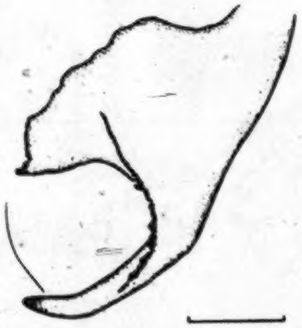
71. *Goniocera io*



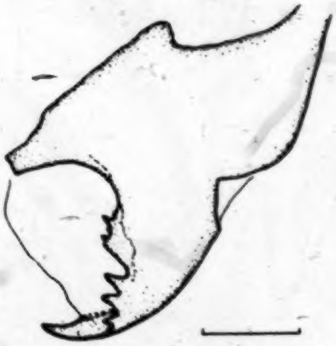
72. *Goniocera versicolor*



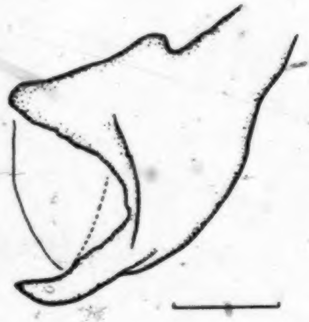
73. *Proceromyia macronychia*



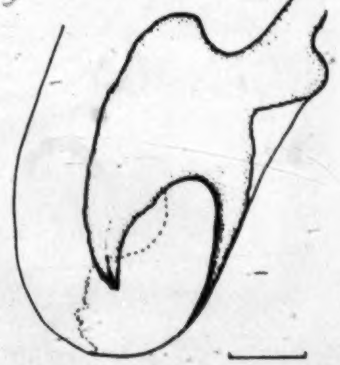
74. *Proceromyia pubioculata*



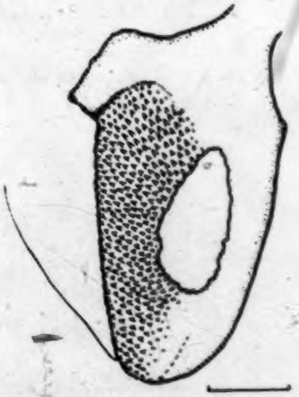
75. *Entomophaga exoleta*



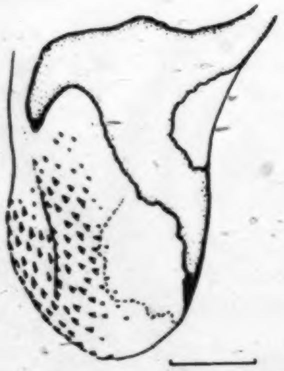
76. *Entomophaga nigrohalterata*



77. *Ceromya flaviceps*



78. *Ceromya* New Guinea sp. 6



79. *Ceromya americana* complex

Figures 80 to 88. Lateral view of male pregonite. Scale bars = 0.05mm.

Figure 80. *Ceromya cornuta* (Y114, CNC).

Figure 81. *Ceromya* Mexico sp. 5 (Y118, CNC).

Figure 82. *Ceromya* Brazil sp. 3 (Y125, INPA).

Figure 83. *Ceromya lutea* (Y121, CNC).

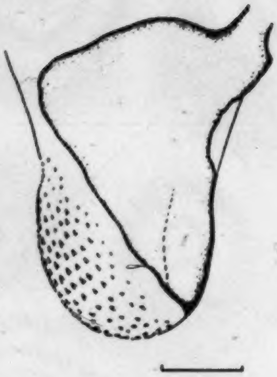
Figure 84. *Ceromya silacea* (Y179, CNC).

Figure 85. *Actia lamia* (Y17, JEOH).

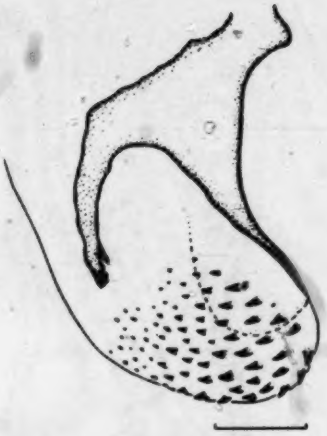
Figure 86. *Actia diffidens* (Y21, CNC).

Figure 87. *Peribaea tibialis* (Y15, JEOH).

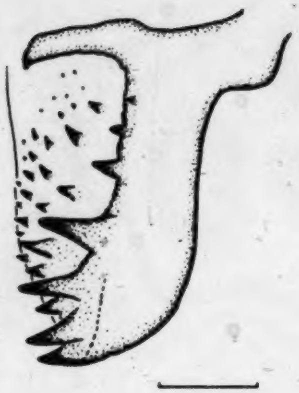
Figure 88. *Peribaea* Australia sp. 3 (Y77, DPI).



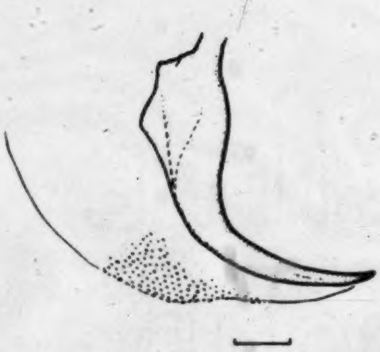
80. *Ceromya cornuta*



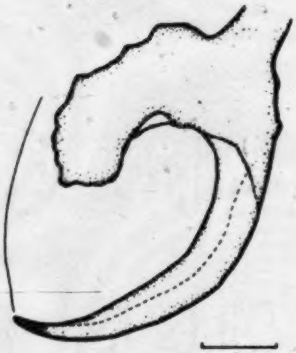
81. *Ceromya* Mexico sp. 5



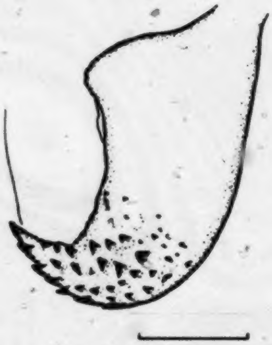
82. *Ceromya* Brazil sp. 3



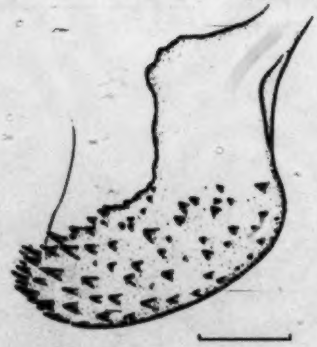
83. *Ceromya lutea*



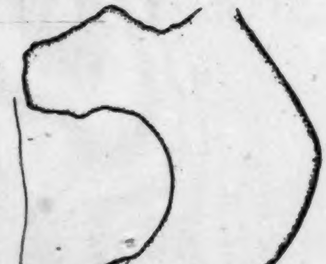
84. *Ceromya silacea*



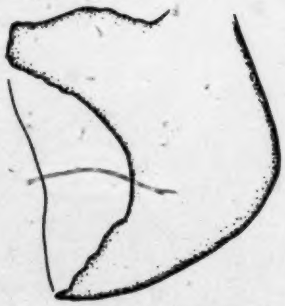
85. *Actia lamia*



86. *Actia diffidens*



87. *Peribaea tibialis*



88. *Peribaea* Australia sp. 3

Figures 89 to 97. Lateral view of male pregonite. Scale bars = 0.05mm.

Figure 89. *Siphona (Actinocrocuta) singularis* complex (O120, CNC).

Figure 90. *Siphona (Aphantorhapha) arizonica* (unnumbered, JEOH).

Figure 91. *Siphona (Aphantorhaphopsis) crassulata* (B3, CNC).

Figure 92. *Siphona (Aphantorhaphopsis) starkei* (B96, JEOH).

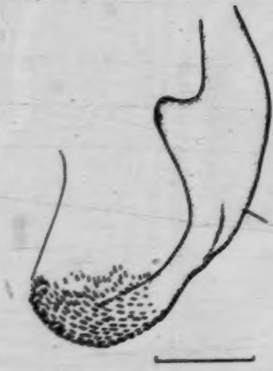
Figure 93. *Siphona (Baeomyia) xanthogaster* (B98, JEOH).

Figure 94. *Siphona (Ceranthia) flavipes* (B8, CNC).

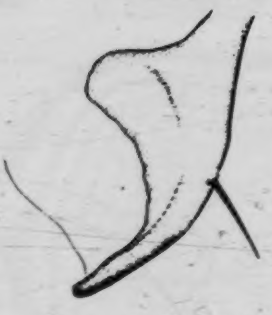
Figure 95. *Siphona (Pseudosiphona) brevirostris* (W89, CNC).

Figure 96. *Siphona (Siphona) geniculata* (W37, JEOH).

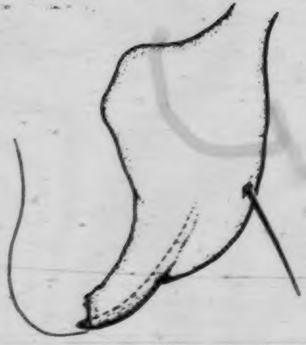
Figure 97. *Siphona (Siphonopsis) plusiae* (R97, JEOH).



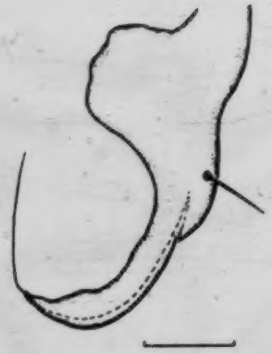
89. *S.* (*Actinocrocuta*) *singularis* complex



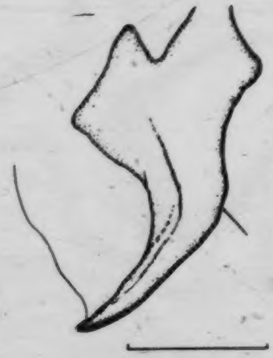
90. *S.* (*Aphantorhapha*) *arizonica*



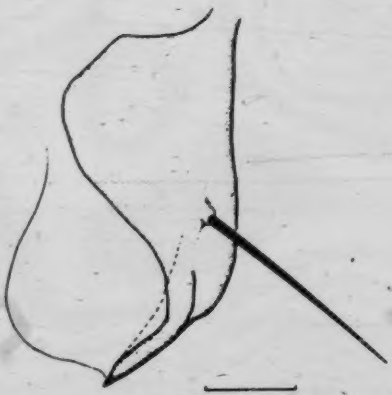
91. *S.* (*Aphantorhaphopsis*) *crassulata*



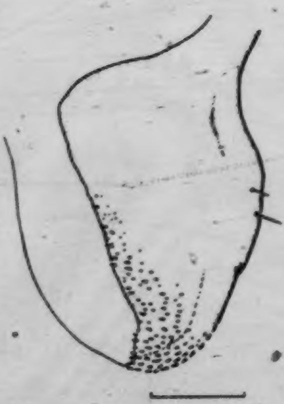
92. *S.* (*Aphantorhaphopsis*) *starkei*



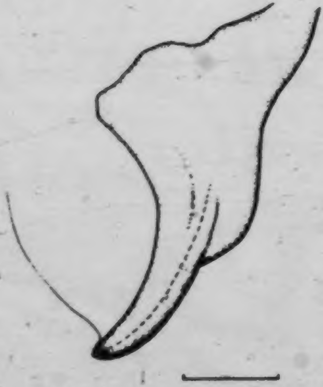
93. *S.* (*Baeomyia*) *xanthogaster*



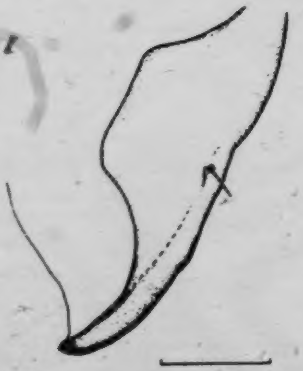
94. *S.* (*Ceranthia*) *flavipes*



95. *S.* (*Pseudosiphona*) *brevirostris*



96. *S.* (*Siphona*) *geniculata*



97. *S.* (*Siphonopsis*) *plusiae*

Figures 98 to 106. Lateral view of male pregonite. Scale bars = 0.05mm.

Figure 98. *Siphona (Siphonopsis)* sp. N (O24, CNC).

Figure 99. *Siphona (Uruactia)* sp. 31 (R45, CNC).

Figure 100. *Siphona s.l.*, sp. grp. 1, sp. 27 (R46, CNC).

Figure 101. *Siphona s.l.*, sp. grp. 1, sp. 28 (O27, CNC).

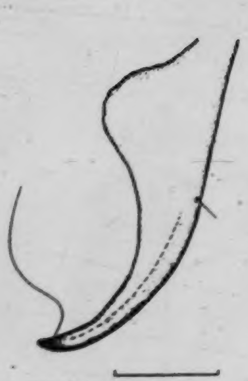
Figure 102. *Siphona s.l.*, sp. grp. 2, sp. 1 (O125, JEOH).

Figure 103. *Siphona s.l.*, sp. grp. 2, sp. 2 (B92, USNM).

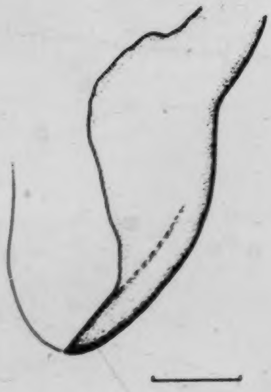
Figure 104. *Siphona s.l.*, sp. grp. 3, sp. 3 (B81, WSUP).

Figure 105. *Siphona s.l.*, sp. grp. 3, sp. 22 (O50, USP).

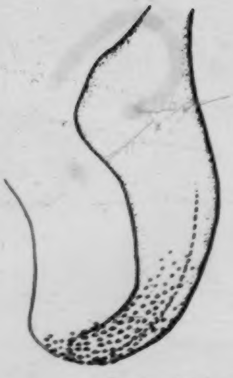
Figure 106. *Siphona s.l.*, unplaced sp. 1 (R62, WSUP).



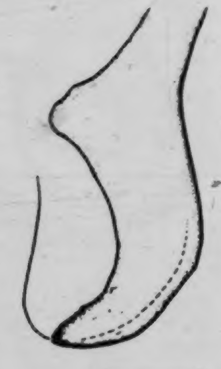
98. *S. (Siphonopsis)* sp. 14



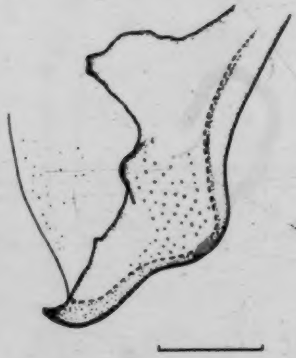
99. *S. (Uruactia)* sp. 31



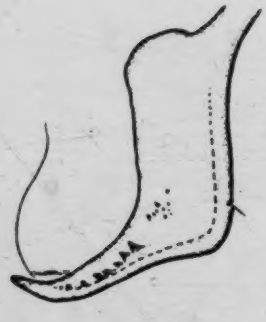
100. *Siphona s.l.*, sp. grp. 1, sp. 27



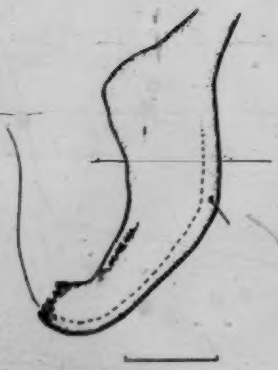
101. *Siphona s.l.*, sp. grp. 1, sp. 28



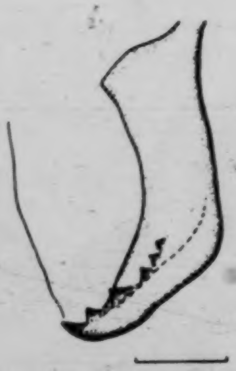
102. *Siphona s.l.*, sp. grp. 2, sp. 1



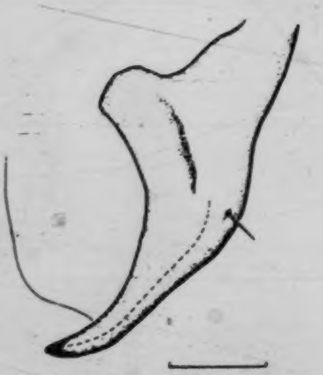
103. *Siphona s.l.*, sp. grp. 2, sp. 2



104. *Siphona s.l.*, sp. grp. 3, sp. 3



105. *Siphona s.l.*, sp. grp. 3, sp. 22



106. *Siphona s.l.*, unplaced sp. 1

Figures 107 to 112. Lateral view of male distiphallus. Scale bars = 0.05mm.

Figure 107. *Goniocera io* (Y41, CNC).

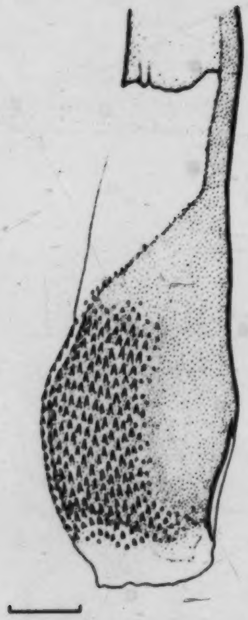
Figure 108. *Proceromyia macronychia* (Y40, CNC).

Figure 109. *Proceromyia pubioculata* (Y85, JEOH).

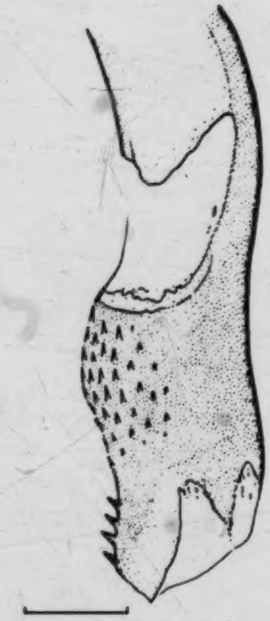
Figure 110. *Entomophaga exoleta* (Y132, ZMUC).

Figure 111. *Entomophaga nigrohalterata* (Y27, CNC).

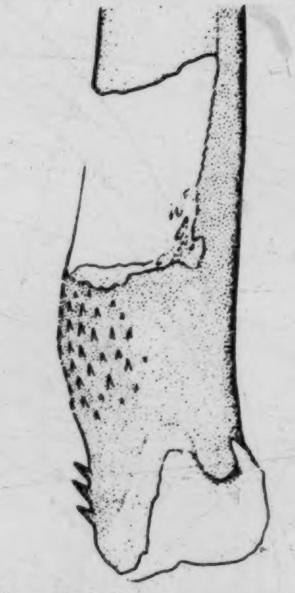
Figure 112. *Ceromya silacea* (Y179, CNC).



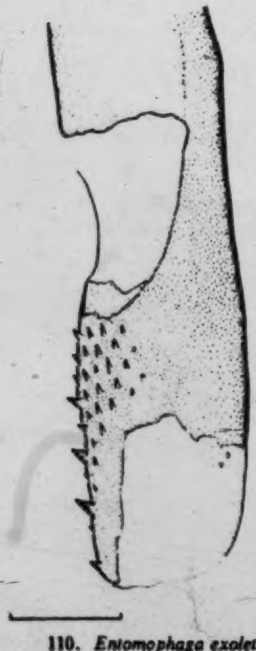
107. *Goniocera io*



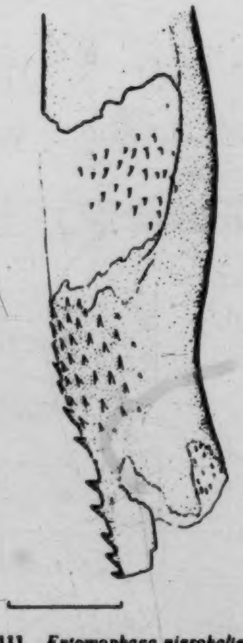
108. *Proceromyia macronychia*



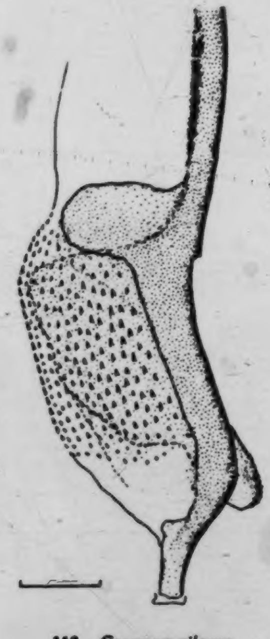
109. *Proceromyia pubioculata*



110. *Entomophaga exoleta*



111. *Entomophaga nigrohalterata*



112. *Ceromya silacea*

Figures 113 to 118. Lateral view of male distiphallus. Scale bars = 0.05mm.

Figure 113. *Ceromya flaviceps* (Y107, CNC).

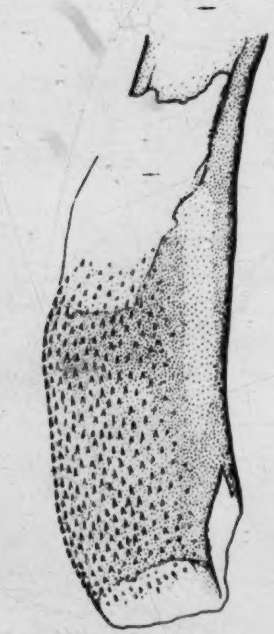
Figure 114. *Ceromya americana* complex (Y25, CNC).

Figure 115. *Ceromya cornuta* (Y114, CNC).

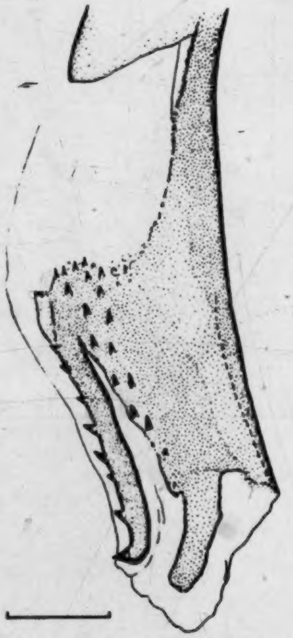
Figure 116. *Ceromya lutea* (Y121, CNC).

Figure 117. *Actia lamia* (Y17, JEOH).

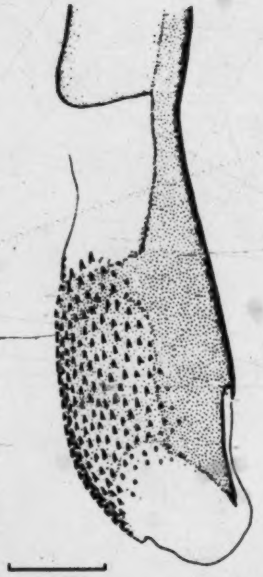
Figure 118. *Actia autumnalis* (Y22, CNC).



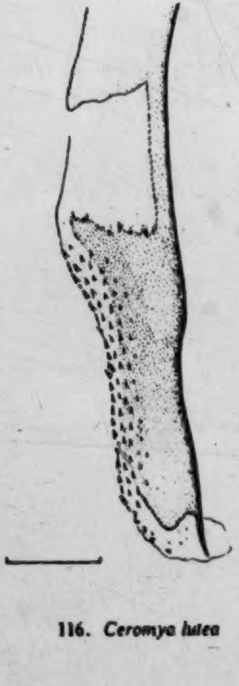
113. *Ceromya flaviceps*



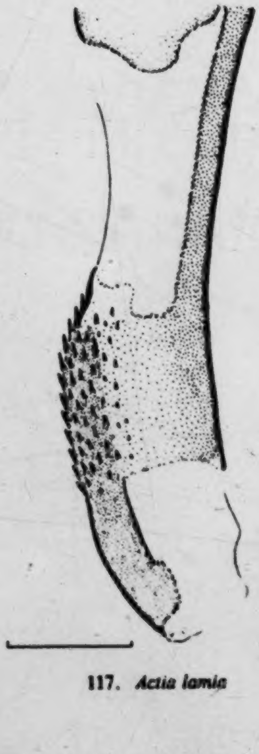
114. *Ceromya americana* complex



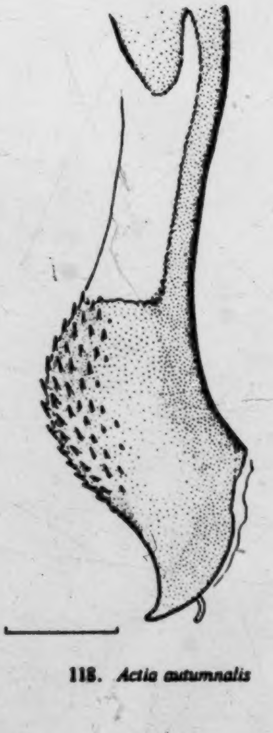
115. *Ceromya cornuta*



116. *Ceromya lutea*



117. *Actia lamia*



118. *Actia autumnalis*

Figures 119 to 124. Lateral view of male distiphallus. Scale bars = 0.05mm.

Figure 119. *Actia* New World sp. 4 (Y48, USP).

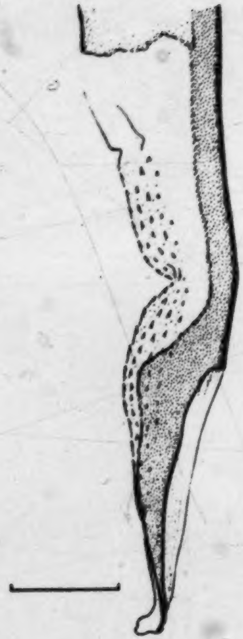
Figure 120. *Peribaea apicalis* (Y82, CNC).

Figure 121. *Peribaea fissicornis* (Y31, CNC).

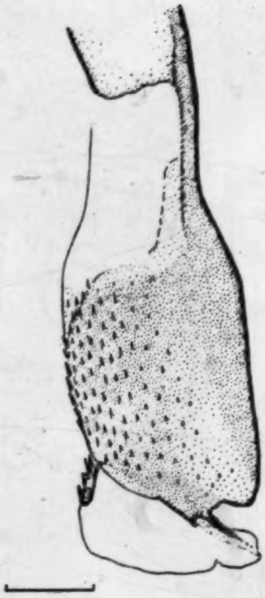
Figure 122. *Siphona (Actinocrocuta) singularis* complex (O120, CNC).

Figure 123. *Siphona (Actinocrocuta)* sp. 1 (R4, CNC).

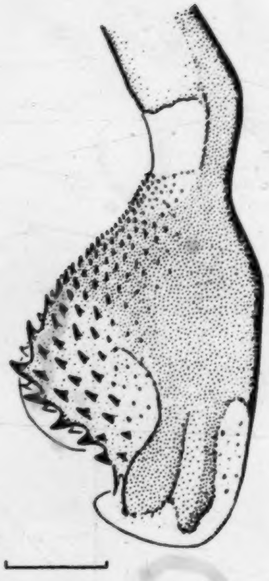
Figure 124. *Siphona (Aphantorhapha) arizonica* (unnumbered, JEOH).



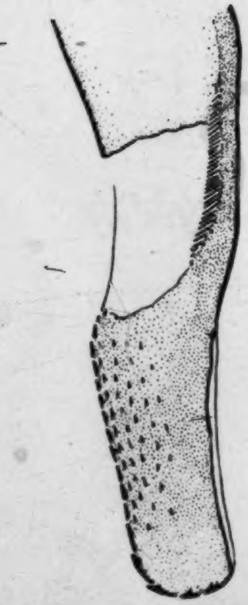
119. ***Actia*** **New World sp. 4**



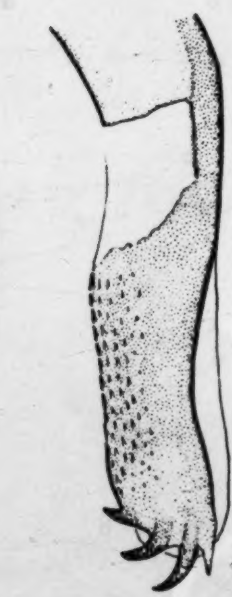
120. ***Peribaea apicalis***



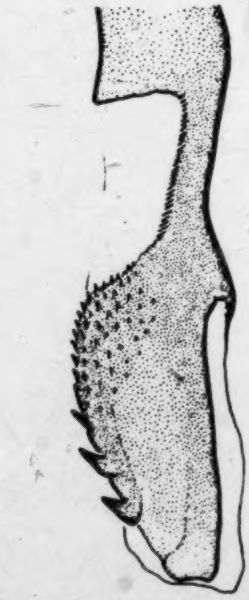
121. ***Peribaea fissicornis***



122. ***S.*** **(*Actinocrocuta*)** ***singularis*** **complex**



123. ***S.*** **(*Actinocrocuta*) sp. 1**



124. ***S.*** **(*Aphantorhapha*)** ***arizonica***

Figures 125 to 130. Lateral view of male distiphallus. Scale bars = 0.05mm.

Figure 125. *Siphona (Aphantorhaphopsis) nigronitens* (R13, CNC).

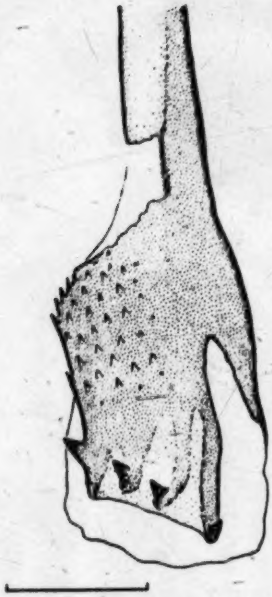
Figure 126. *Siphona (Baeomyia) hurdi* (R10, CNC).

Figure 127. *Siphona (Ceranthia) flavipes* (R81, CNC).

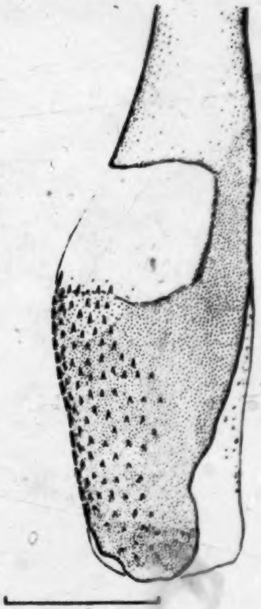
Figure 128. *Siphona (Pseudosiphona)* sp. 1 (B69, CNC).

Figure 129. *Siphona (Siphona) geniculata* (W36, JEOH).

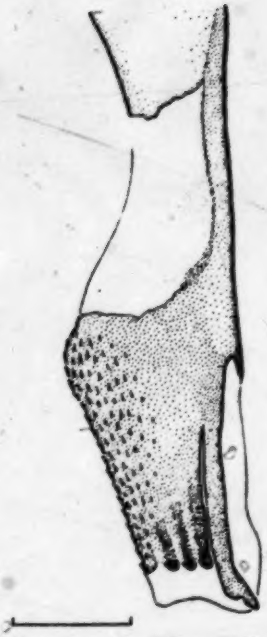
Figure 130. *Siphona (Siphonopsis) plusiae* (B18, CNC).



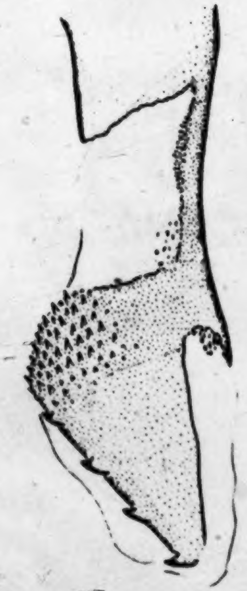
125. *S. (Aphantorhaphopsis) nigronitens*



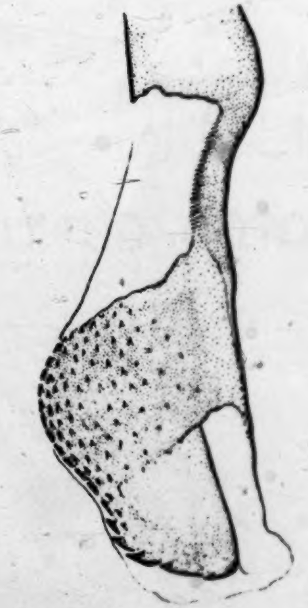
126. *S. (Baeomyia) hurdi*



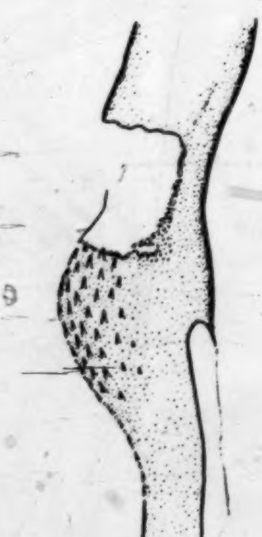
127. *S. (Ceranthia) flavipes*



128. *S. (Pseudosiphona)* sp. 1



129. *S. (Siphona) geniculata*



130. *S. (Siphonopsis) plusiae*

Figures 131 to 136. Lateral view of male distiphallus. Scale bars = 0.05mm.

Figure 131. *Siphona (Uruactia)* sp. 31 (R45, CNC).

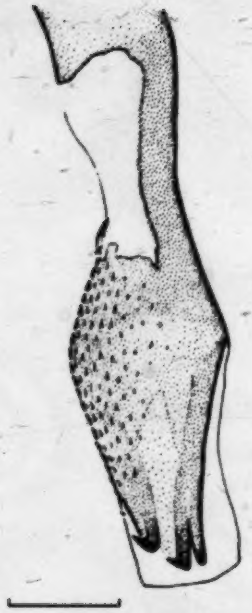
Figure 132. *Siphona s.l.*, sp. grp. 1, sp. 25 (R2, CNC).

Figure 133. *Siphona s.l.*, sp. grp. 2, sp. 1 (O148, CAS).

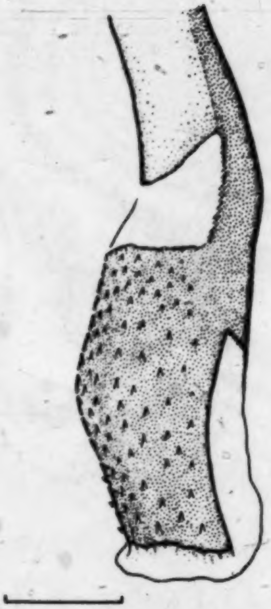
Figure 134. *Siphona s.l.*, sp. grp. 2, sp. 3 (R65, CNC).

Figure 135. *Siphona s.l.*, sp. grp. 3, sp. 3 (B81, WSUP).

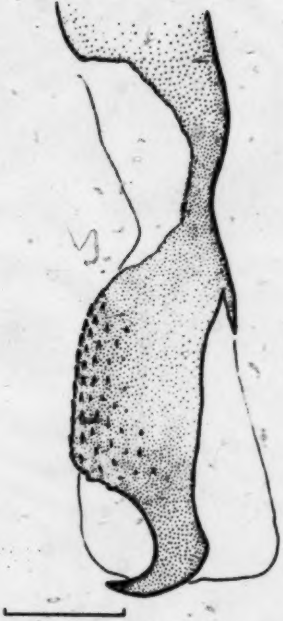
Figure 136. *Siphona s.l.*, unplaced sp. 1 (R62, WSUP).



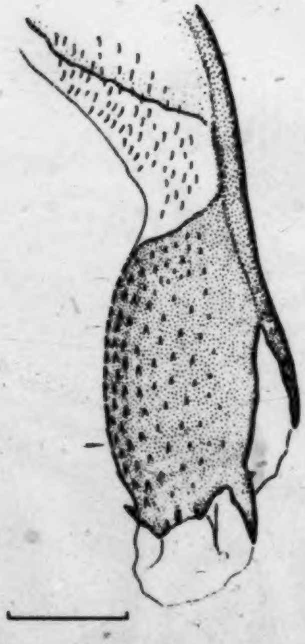
131. *S. (Uruactia)* sp. 31



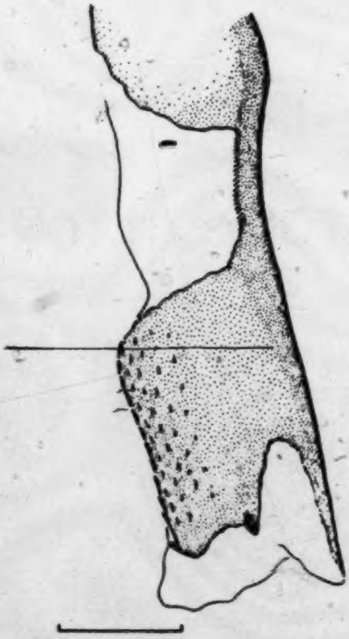
132. *Siphona s.l.*, sp. grp. 1, sp. 25



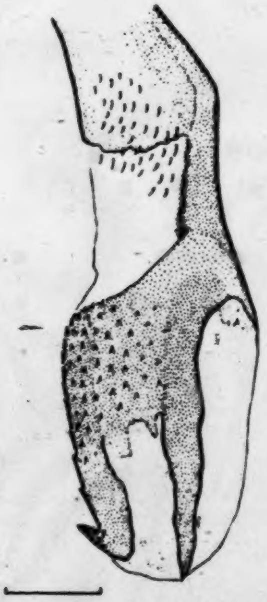
133. *Siphona s.l.*, sp. grp. 2, sp. 1



134. *Siphona s.l.*, sp. grp. 2, sp. 3



135. *Siphona s.l.*, sp. grp. 3, sp. 3



136. *Siphona s.l.*, unplaced sp. 1

Figures 137 to 141. Lateral view of male surstylus and cerci. Scale bars = 0.1mm.

Figure 137. *Goniocera io* (Y41, CNC).

Figure 138. *Ceromya americana* complex (Y25, CNC).

Figure 139. *Peribaea apicalis* (Y82, CNC).

Figure 140. *Siphona (Pseudosiphona)* sp. 1 (B69, CNC).

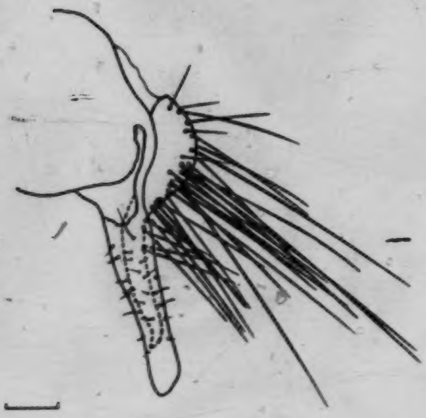
Figure 141. *Siphona (Siphona) geniculata* (W36, JEOH).

Figures 142 to 144. Posterior view of male genitalia, vestiture omitted. Scale bars = 0.1mm.

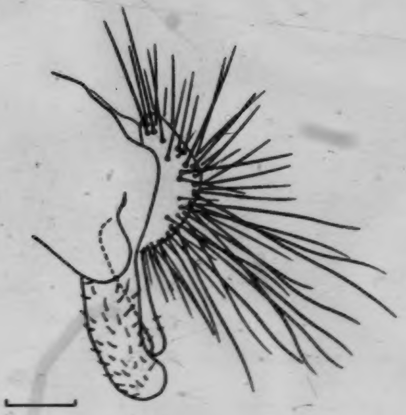
Figure 142. *Siphona (Actinocrocuta) singularis* complex (lectotype of *S. chaetosa* (Tnsd.), USNM).

Figure 143. *Siphona (Aphantorhapha)* sp. 1 (O182, BMNH).

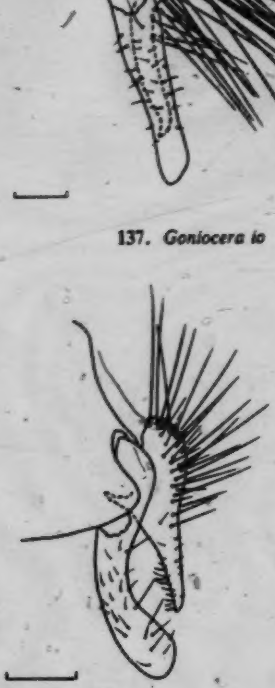
Figure 144. *Siphona (Siphona) kairiensis* (holotype, CAS).



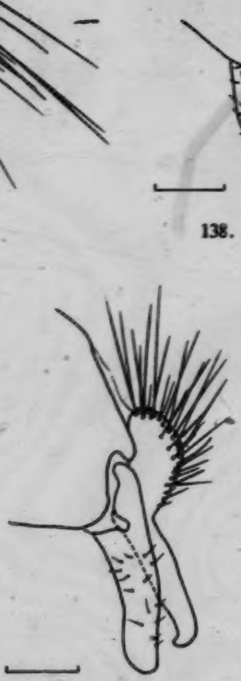
137. *Goniocera io*



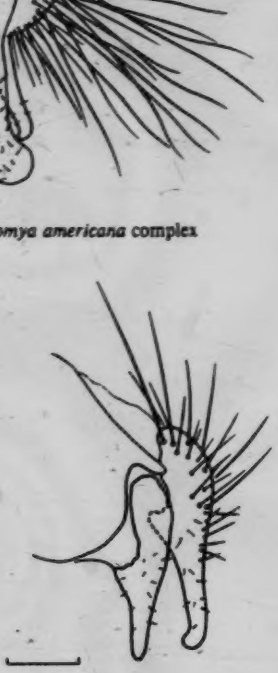
138. *Ceromya americana* complex



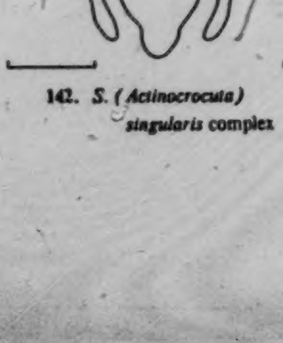
139. *Peribaea apicalis*



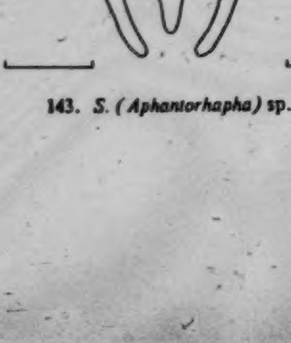
140. *S. (Pseudosiphona)* sp. 1



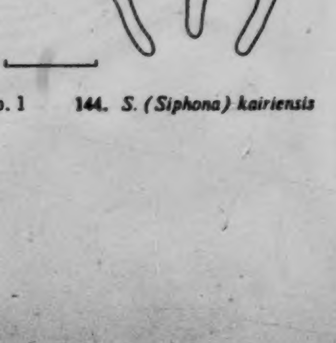
141. *S. (Siphona) geniculata*



142. *S. (Actinocrocuta) singularis* complex



143. *S. (Aphantorhapha)* sp. 1



144. *S. (Siphona) kairiensis*

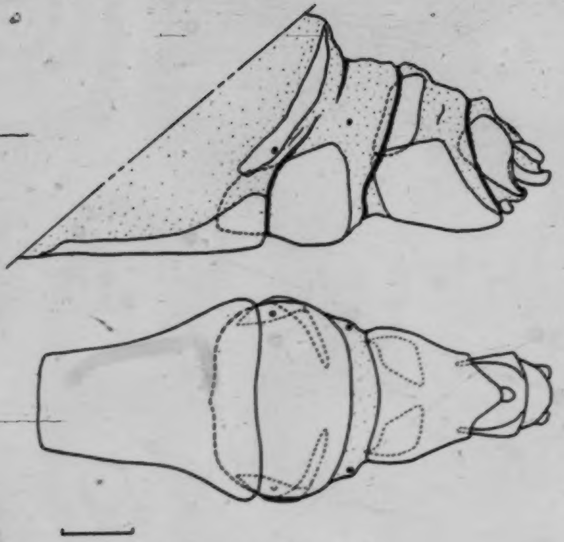
Figures 145 to 148. Lateral and ventral views of female genitalia. Scale bars = 0.2mm.

Figure 145. *Goniocera io* (Y63, CNC).

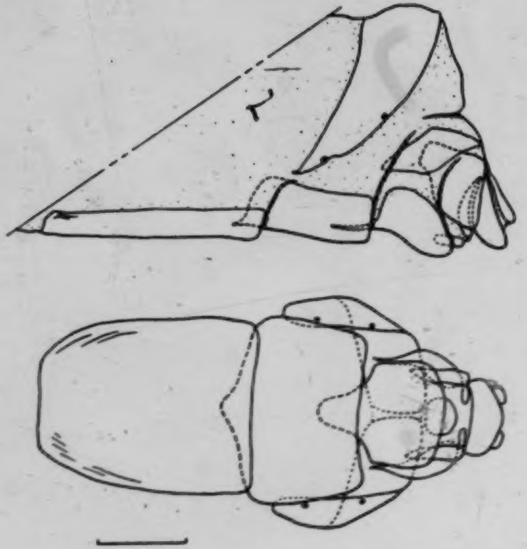
Figure 146. *Proceromyia macronychia* (Y134, CNC).

Figure 147. *Entomophaga nigrohalterata* (Y135, CNC).

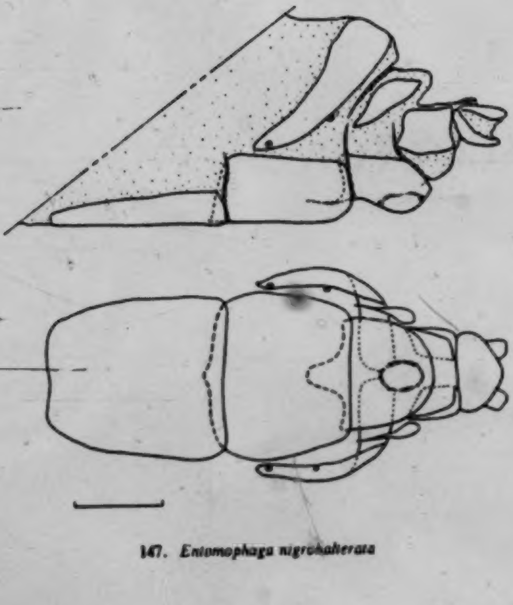
Figure 148. *Ceromya silacea* (Y137, CNC).



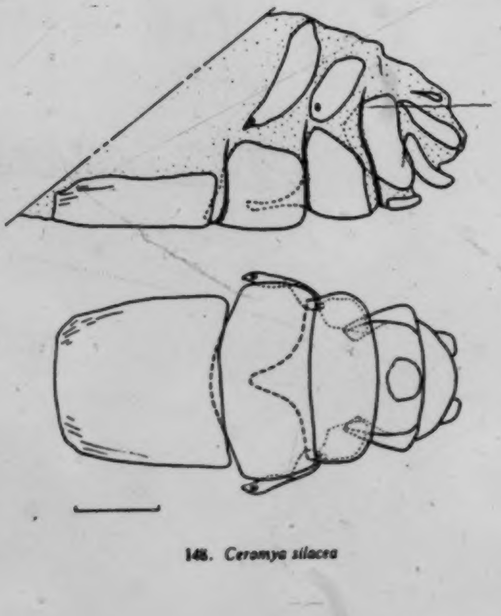
145. *Goniocera io*



146. *Proceromyia macronychia*



147. *Entomophaga nigrohalterata*



148. *Ceromya silacea*

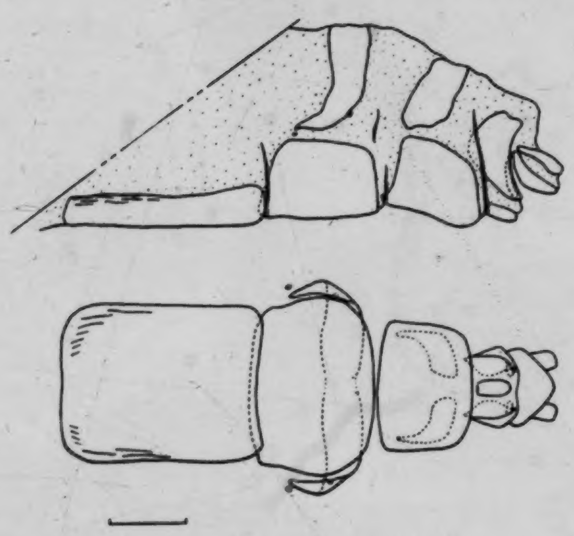
Figures 149 to 152. Lateral and ventral views of female genitalia. Scale bars = 0.2mm.

Figure 149. *Ceromya flaviceps* (Y133, CNC).

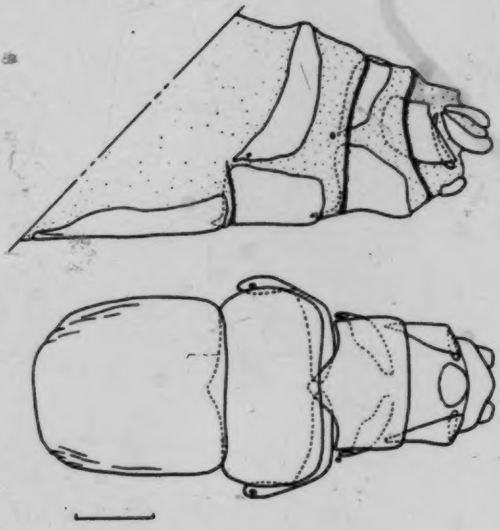
Figure 150. *Ceromya ontario* (Y65, USNM).

Figure 151. *Actia interrupta* (Y74, JEOH).

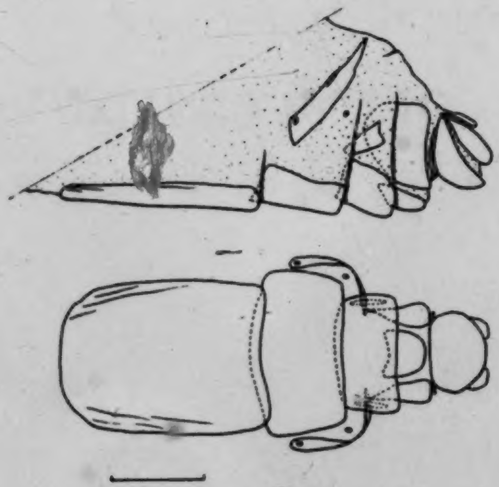
Figure 152. *Actia* Zaire sp. 1 (Y105, CNC).



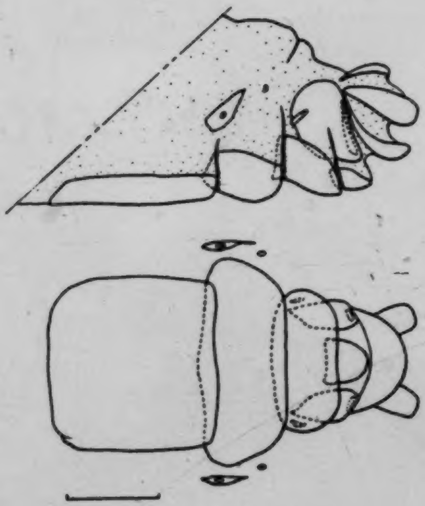
149. *Ceromya flaviceps*



150. *Ceromya ontario*



151. *Actia interrupta*



152. *Actia* Zaire sp. I

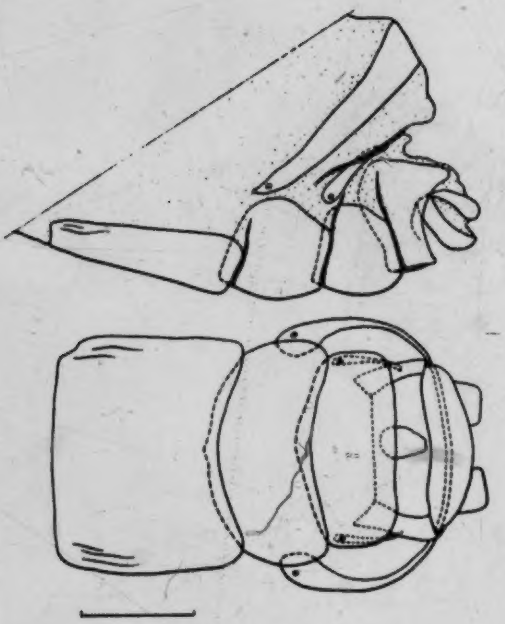
Figures 153 to 156. Lateral and ventral views of female genitalia. Scale bars = 0.2mm.

Figure 153. *Peribaea fissicornis* (Y60, JEOH).

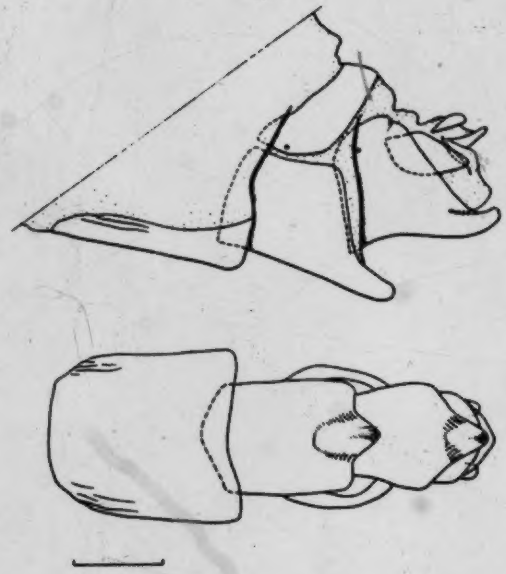
Figure 154. *Peribaea* Africa sp. 5 (Y96, USNM).

Figure 155. *Peribaea ugandana* (Y93, USNM).

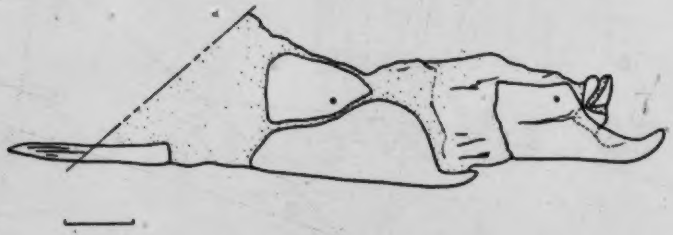
Figure 156. *Peribaea* Australia sp. 1 (Y84, DPI).



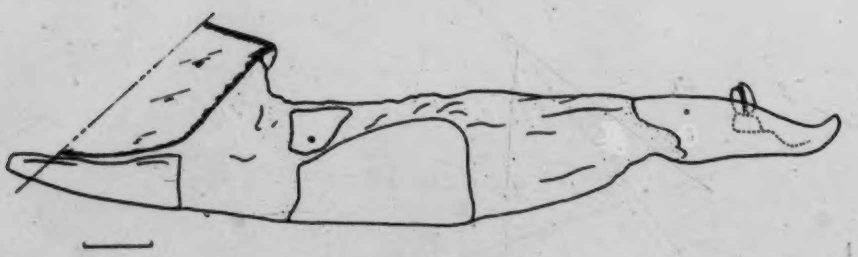
153. *Peribaea fissicornis*



154. *Peribaea* Africa sp. 5



155. *Peribaea ugandana*

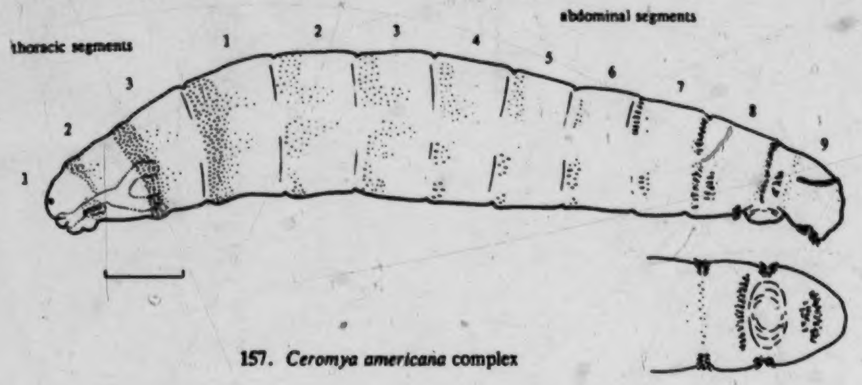


156. *Peribaea* Australia sp. 1

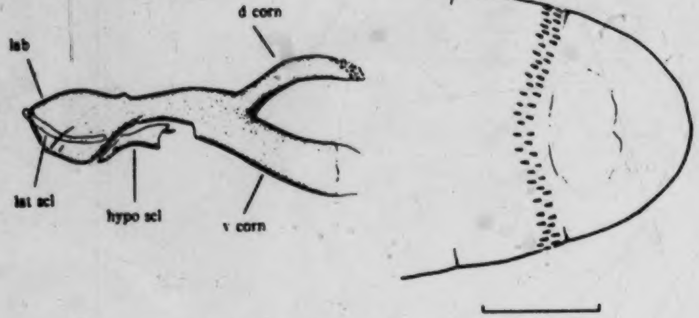
Figure 157. Lateral view of first instar of *Ceromya americana* complex, with ventral view of abdominal segments 7 to 9 (Y73, UCB). Scale bar = 0.1mm.

Figure 158. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instar *Goniocera io* (CNC slide). Abbreviations: d corn, dorsal cornu; hypo scl, hypopharyngeal sclerite; lat scl, lateral sclerite; lab, labrum; v corn, ventral cornu. Scale bar = 0.05mm.

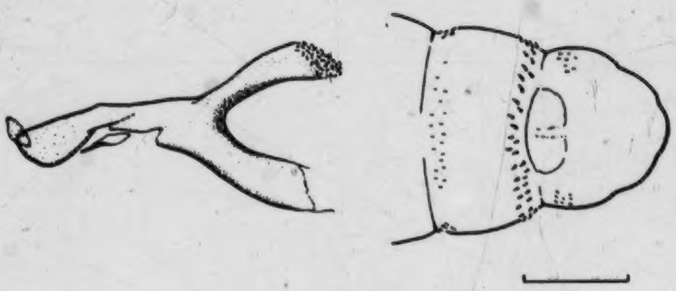
Figure 159. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instar *Entomophaga nigrohalterata* (Y135, CNC). Scale bar = 0.05mm.


thoracic segments
abdominal segments
1
2
3
1
2
3
4
5
6
7
8
9

157. *Ceromya americana* complex


lab
d corn
lat scl
hypo scl
v corn

158. *Goniocera io*



159. *Entomophaga nigrohalterata*

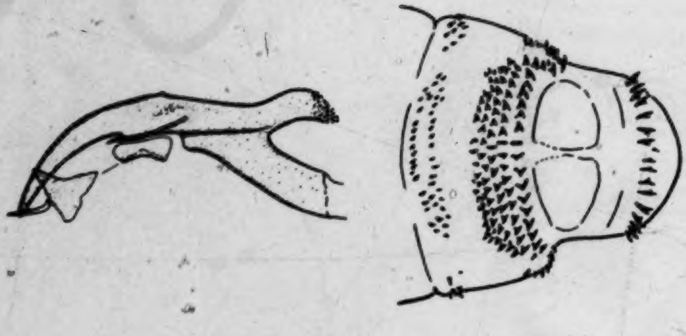
Figures 160 to 163. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 160. *Ceromya silacea* (Y137, CNC).

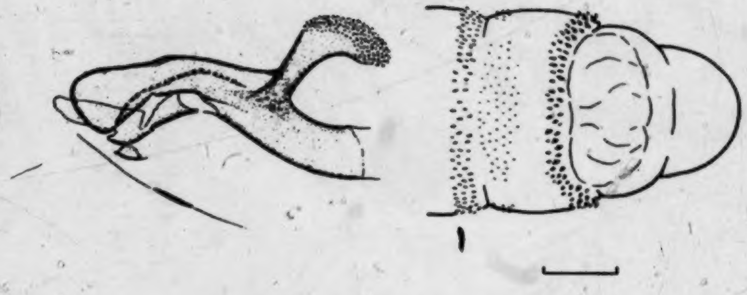
Figure 161. *Ceromya palloris* (Y186, MSU).

Figure 162. *Ceromya americana* complex (Y72, MSU).

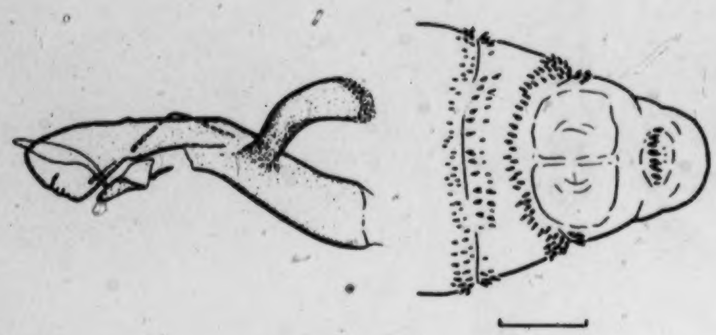
Figure 163. *Ceromya americana* complex (Y73, UCB).



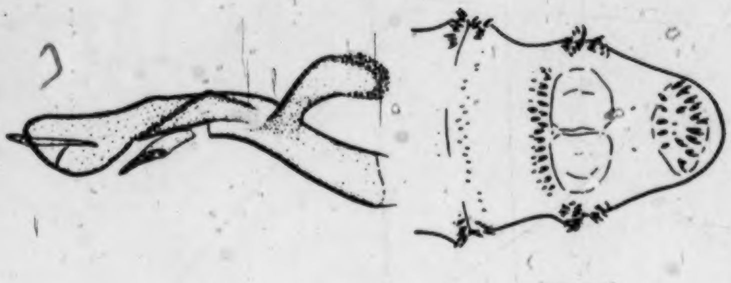
160. *Ceromya silacea*



161. *Ceromya palloris*



162. *Ceromya americana* complex



163. *Ceromya americana* complex

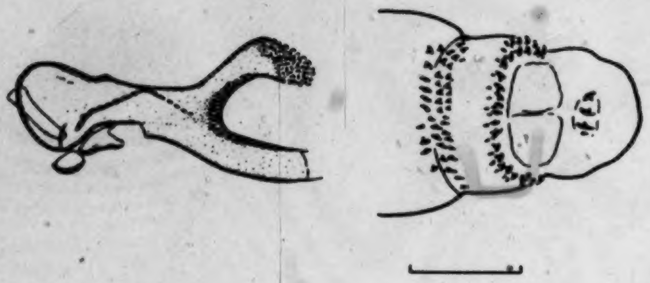
Figures 164 to 167. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 164. *Ceromya* Australia sp. 3 (Y136, DPI).

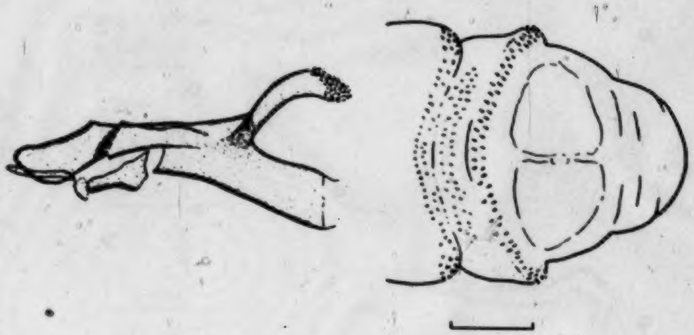
Figure 165. *Ceromya* Nepal sp. 4 (Y139, CNC).

Figure 166. *Ceromya* Chile sp. 1 (Y184, CNC).

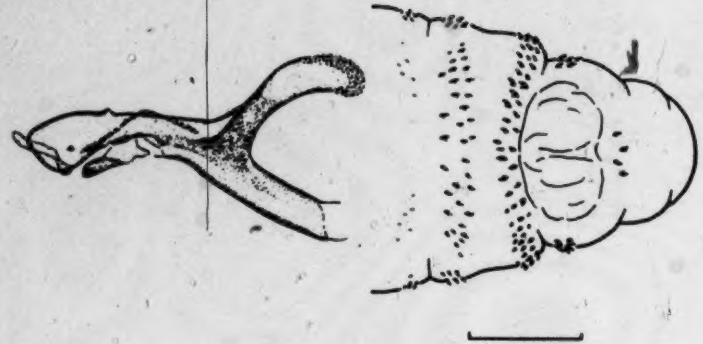
Figure 167. *Ceromya* Brazil sp. 5 (Y185, USP).



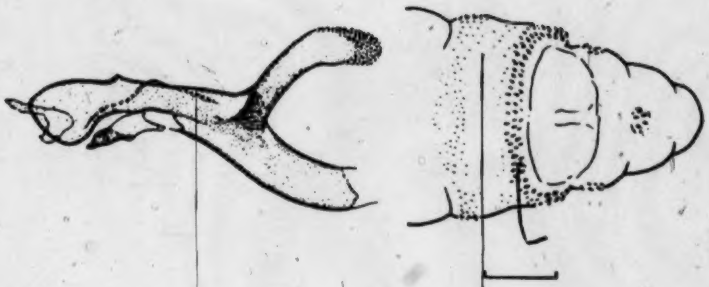
164. *Ceromya* Australia sp. 3



165. *Ceromya* Nepal sp. 4



166. *Ceromya* Chile sp. 1



167. *Ceromya* Brazil sp. 5

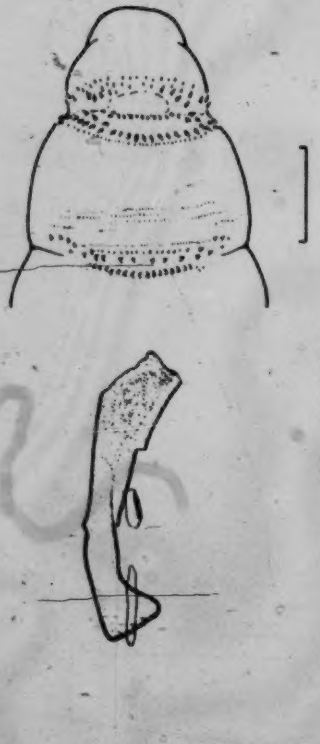
Figures 168 to 171. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 168. *Actia diffidens* (Y64, CNC).

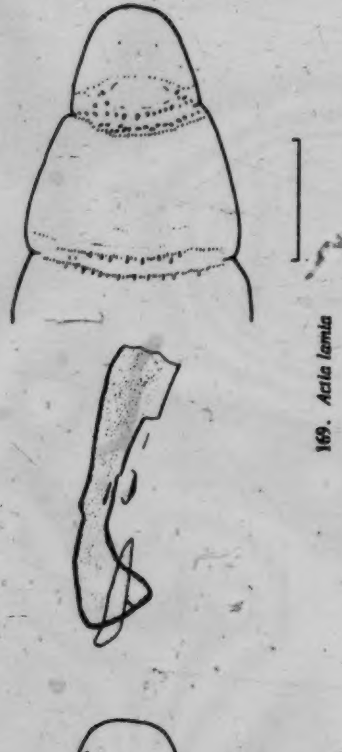
Figure 169. *Actia lamia* (Y75, CNC).

Figure 170. *Actia malaisei* (Y104, CNC).

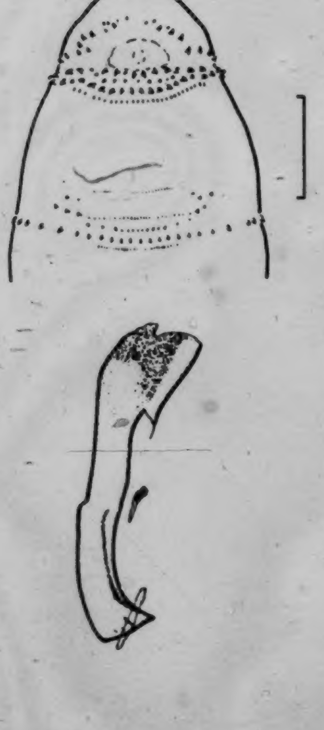
Figure 171. *Actia* nr. *parviseta* (Y173, DPI).



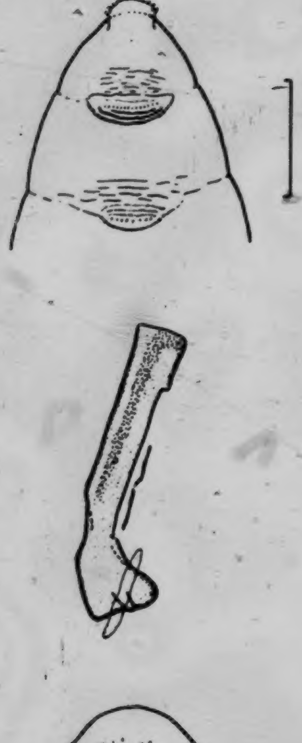
168. *Actia diffidens*



169. *Actia lamia*



170. *Actia malaisei*



171. *Actia* nr. *parviseta*

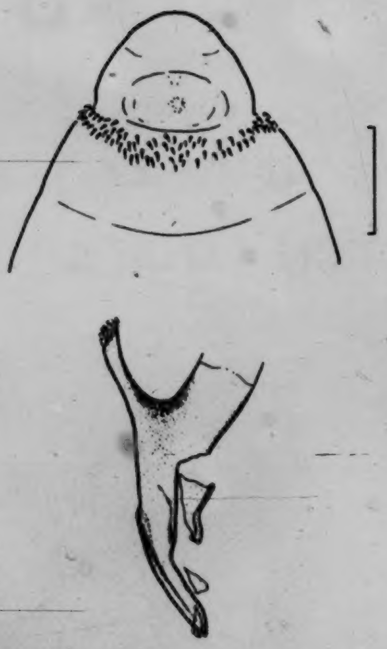
Figures 172 to 175. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 172. *Peribaea ugandana* (Y93, USNM).

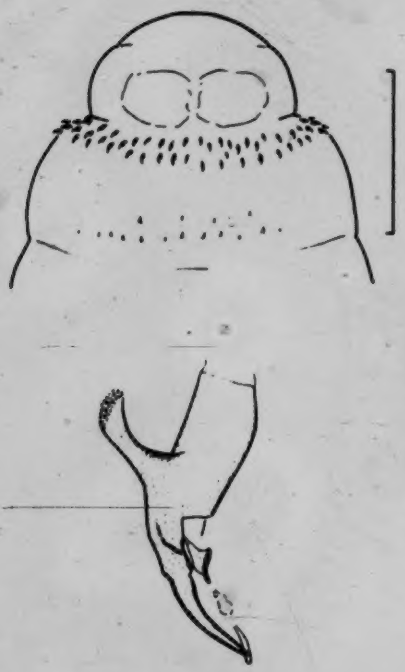
Figure 173. *Peribaea* Africa sp. 3 (Y91, CAS).

Figure 174. *Peribaea* Africa sp. 4 (Y62, USNM).

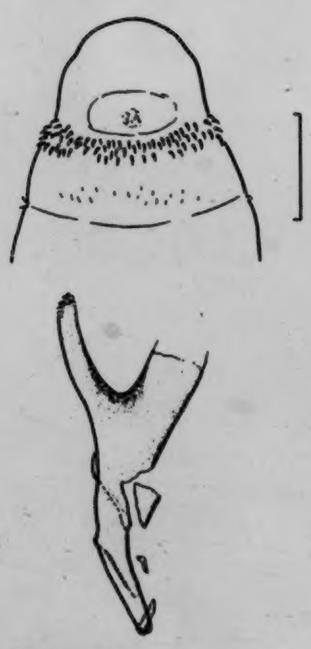
Figure 175. *Peribaea* Africa sp. 5 (Y96, USNM).



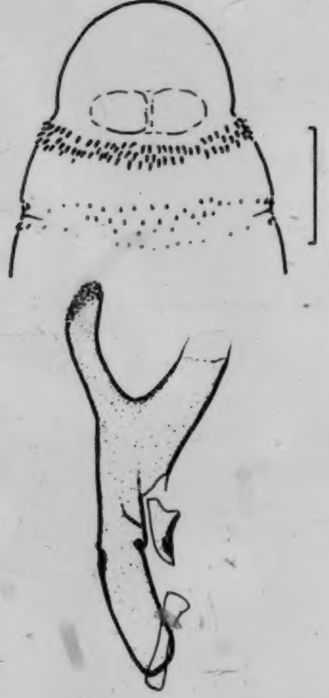
172. *Peribaea ugandana*



173. *Peribaea* Africa sp. 3



174. *Peribaea* Africa sp. 4



175. *Peribaea* Africa sp. 5

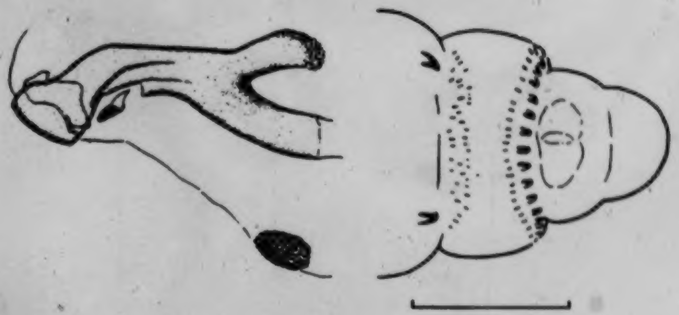
Figures 176 to 179. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 176. *Siphona (Aphantorhaphopsis)* Australia sp. 1 (R90, DPI).

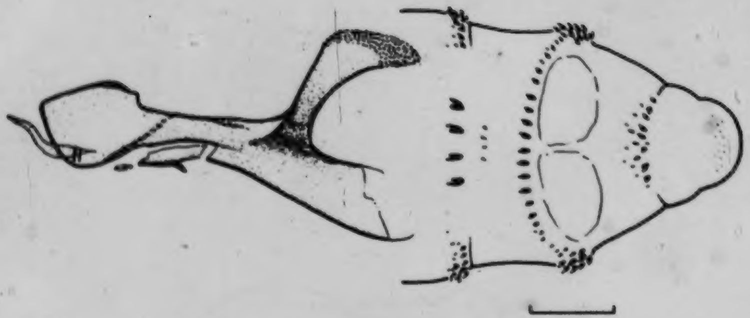
Figure 177. *Siphona (Aphantorhaphopsis)* Kenya sp. 1 (O167, USNM).

Figure 178. *Siphona (Aphantorhaphopsis)* Nepal sp. 1 (W84, CNC).

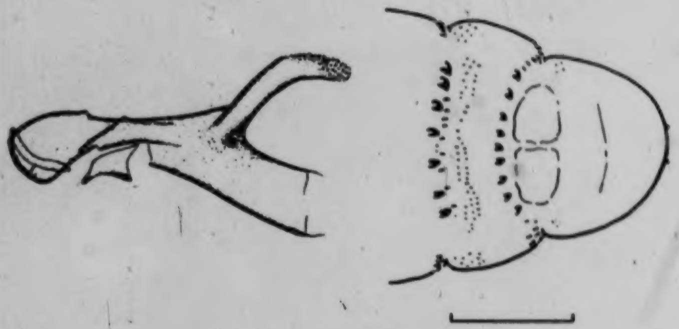
Figure 179. *Siphona (Aphantorhaphopsis)* Nepal sp. 4 (O174, CNC).



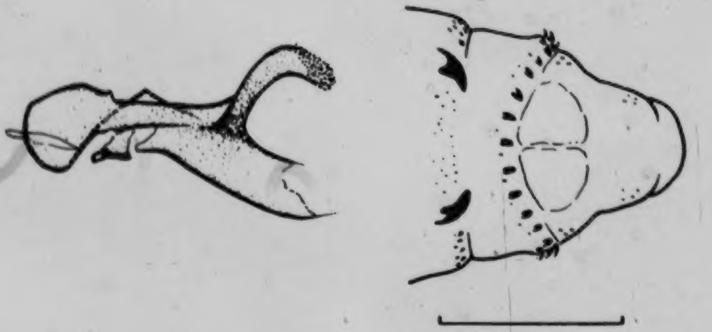
176. *S. (Aphantorhaphopsis)* Australia sp. 1



177. *S. (Aphantorhaphopsis)* Kenya sp. 1



178. *S. (Aphantorhaphopsis)* Nepal sp. 1



179. *S. (Aphantorhaphopsis)* Nepal sp. 4

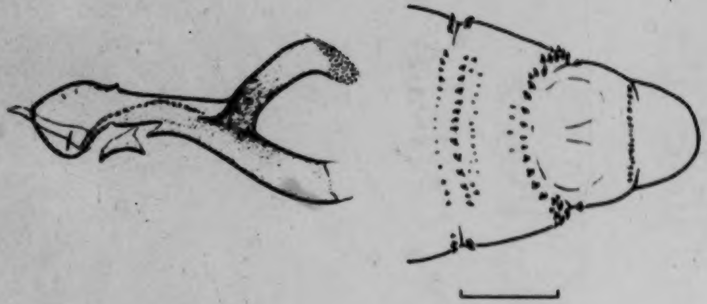
Figures 180 to 183. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 180. *Siphona (Aphantorhaphopsis)* Uganda sp. 1 (O169, CNC).

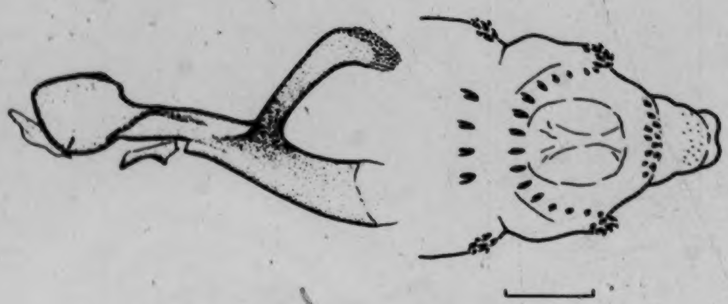
Figure 181. *Siphona (Aphantorhaphopsis)* South Africa sp. 1 (O165, USNM).

Figure 182. *Siphona (Actinocrocuta) singularis* complex (O130, CNC).

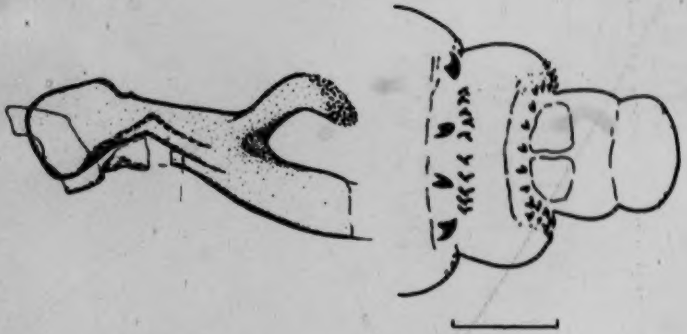
Figure 183. *Siphona (Aphantorhapha) arizonica* (unnumbered, JEOH).



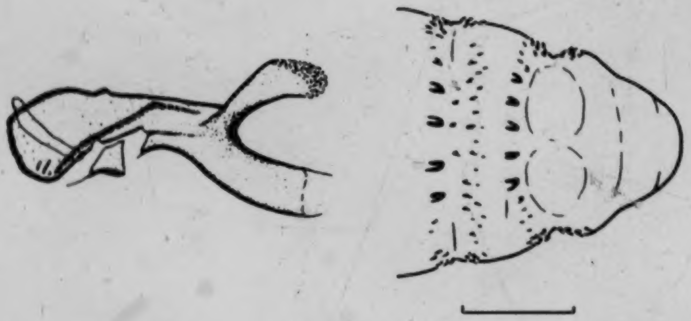
180. *S. (Aphantorhaphopsis)* Uganda sp. 1



181. *S. (Aphantorhaphopsis)* South Africa sp. 1



182. *S. (Actinocrocuta) singularis* complex



183. *S. (Aphantorhapha) arizonica*

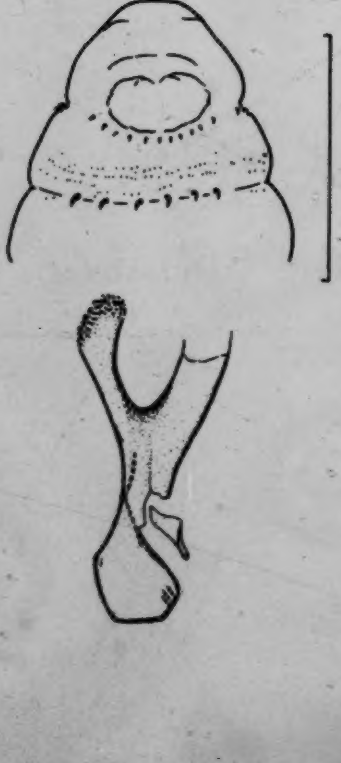
Figures 184 to 187. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 184. *Siphona (Baeomyia) sonorensis* (O133, JEOH).

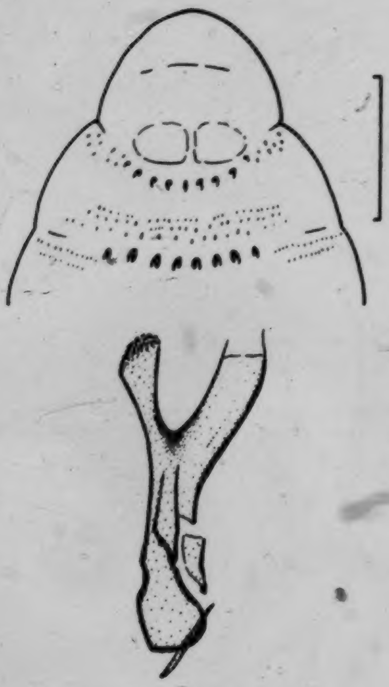
Figure 185. *Siphona (Ceranthia) flavipes* (R67, CNC).

Figure 186. *Siphona (Ceranthia)* U.S. sp. 1 (R89, PHA).

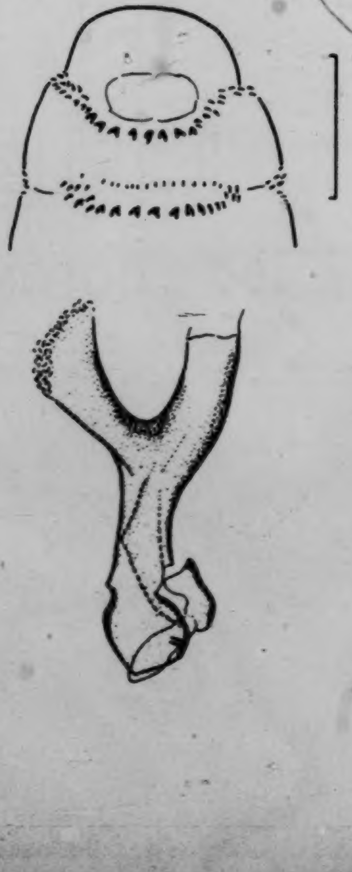
Figure 187. *Siphona (Ceranthia)* U.S. sp. 7 (O158, USNM).



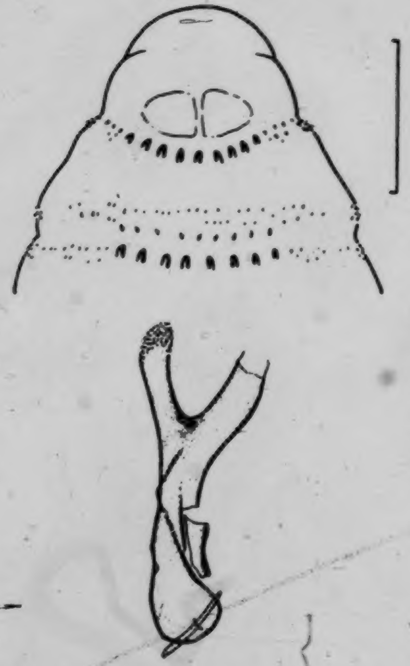
184. *S. (Baeomyia) sonorensis*



185. *S. (Ceranthia) flavipes*



186. *S. (Ceranthia)* U.S. sp. 1



187. *S. (Ceranthia)* U.S. sp. 7

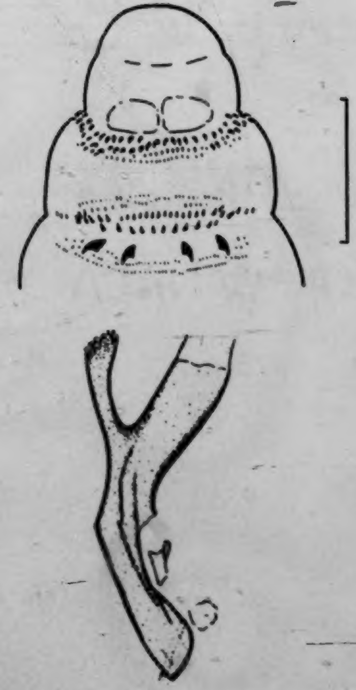
Figures 188 to 191. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 188. *Siphona (Pseudosiphona)* sp. 1 (R33, CNC).

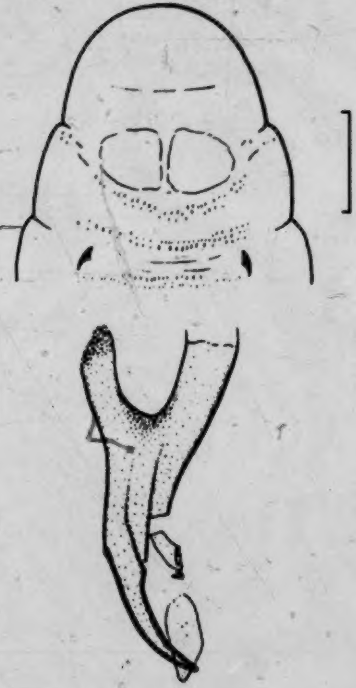
Figure 189. *Siphona (Pseudosiphona)* sp. 2 (R58, CNC).

Figure 190. *Siphona (Pseudosiphona)* sp. 14 (B93, CNC).

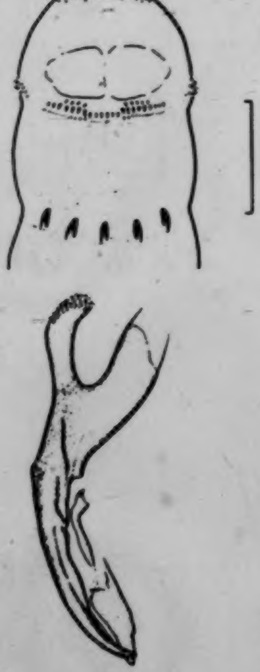
Figure 191. *Siphona (Pseudosiphona)* sp. 15 (R37, CNC).



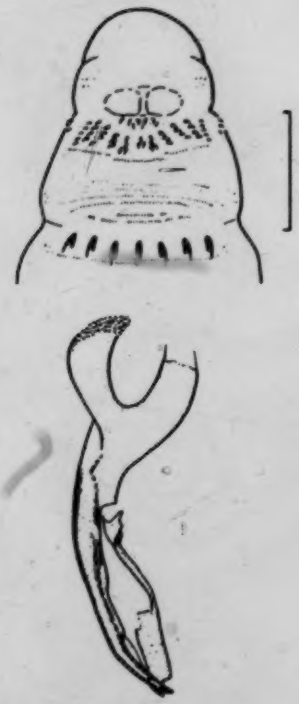
188. *S. (Pseudosiphona)* sp. 1



189. *S. (Pseudosiphona)* sp. 2



190. *S. (Pseudosiphona)* sp. 14



191. *S. (Pseudosiphona)* sp. 15

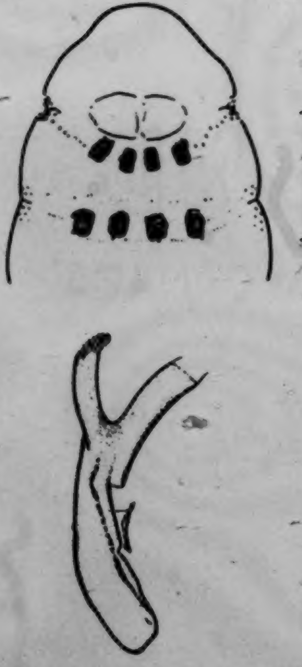
Figures 192 to 195. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 192. *Siphona (Pseudosiphona)* sp. 16 (B88, CNC).

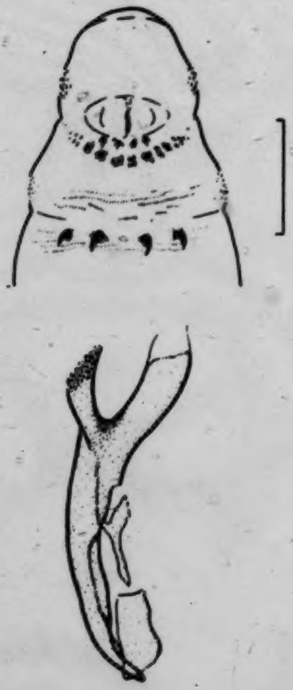
Figure 193. *Siphona (Pseudosiphona)* sp. 17 (O191, BMNH).

Figure 194. *Siphona (Siphonopsis) plusiae* (R7, PHA).

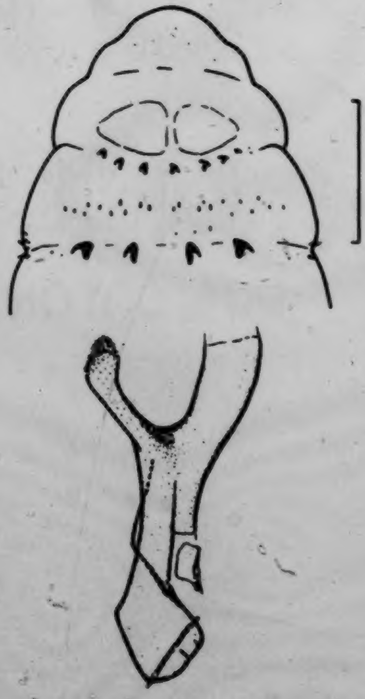
Figure 195. *Siphona (Siphonopsis) conata* (R8, PHA).



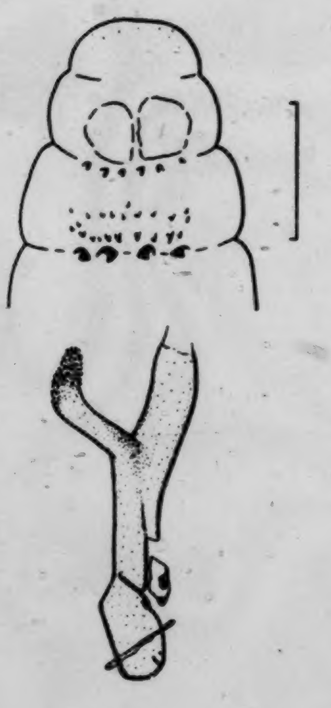
192. *S. (Pseudosiphona)* sp. 16



193. *S. (Pseudosiphona)* sp. 17



194. *S. (Siphonopsis) plusiae*



195. *S. (Siphonopsis) conata*

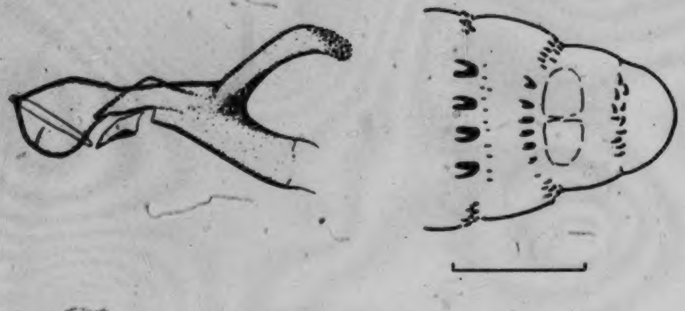
Figures 196 to 199. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 196. *Siphona (Siphona) lutea* (W44, CNC).

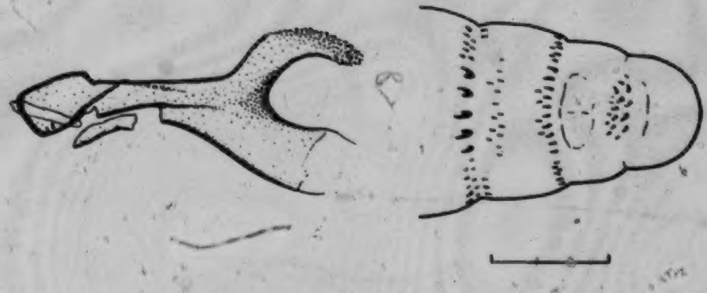
Figure 197. *Siphona (Siphona) nigricans* (W31, CNC).

Figure 198. *Siphona (Siphona)* sp. 1 (W82, JEOH).

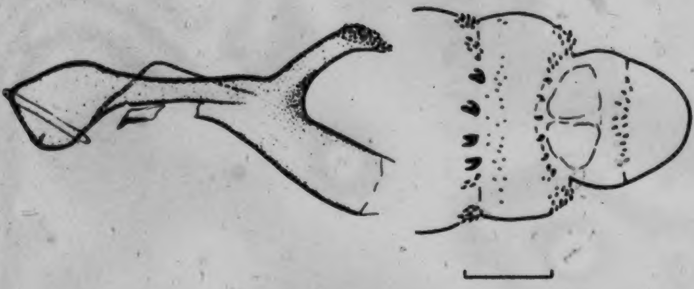
Figure 199. *Siphona s.l.*, sp. grp. 1, sp. 24 (O192, CNC).



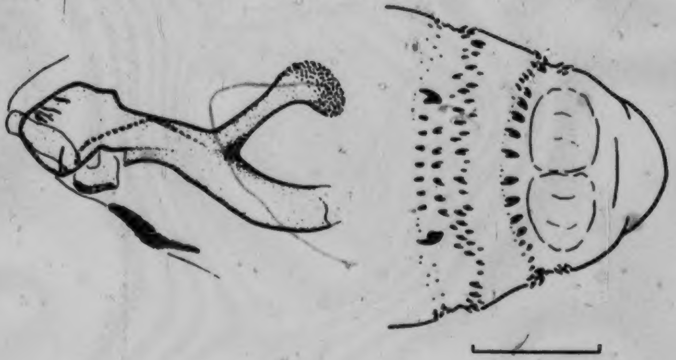
196. *S. (Siphona) lutea*



197. *S. (Siphona) nigricans*



198. *S. (Siphona)* sp. 1



199. *Siphona s.l.*, sp. grp. 1, sp. 24

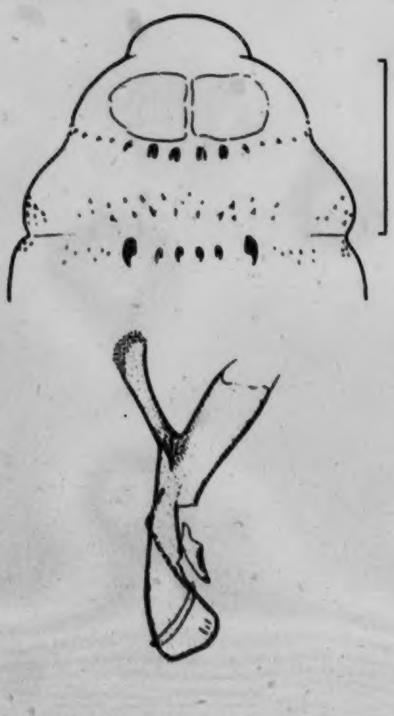
Figures 200 to 203. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 200. *Siphona s.l.*, sp. grp. 1, sp. 27 (O161, CNC).

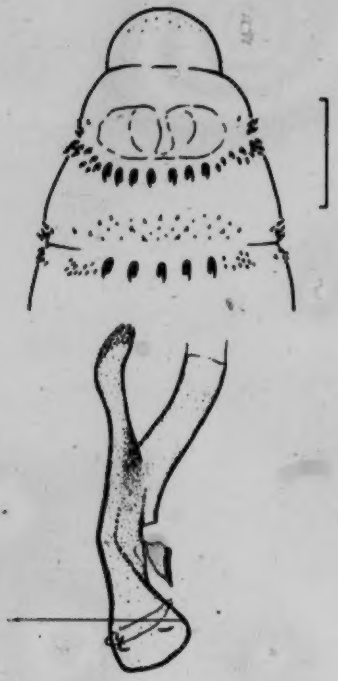
Figure 201. *Siphona s.l.*, sp. grp. 1, sp. 30 (R35, CNC).

Figure 202. *Siphona s.l.*, sp. grp. 2, sp. 3 (R66, CNC).

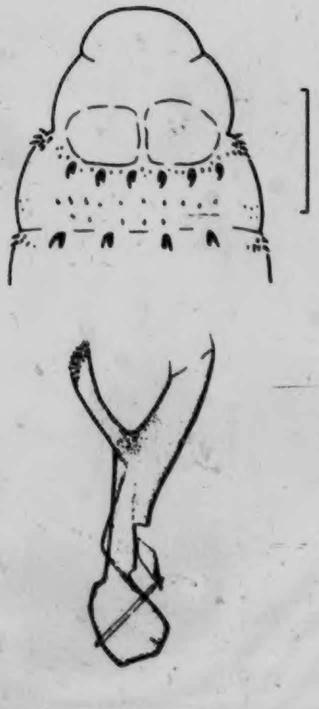
Figure 203. *Siphona s.l.*, sp. grp. 3, sp. 3 (O172, PHA).



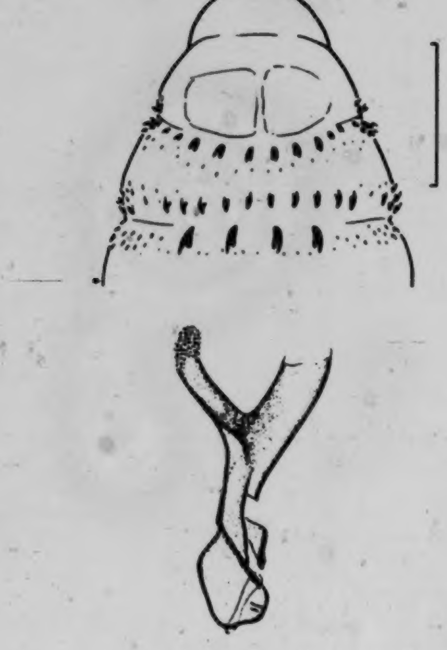
200. *Siphona s.l.*, sp. grp. 1, sp. 27



201. *Siphona s.l.*, sp. grp. 1, sp. 30



202. *Siphona s.l.*, sp. grp. 2, sp. 3



203. *Siphona s.l.*, sp. grp. 3, sp. 3

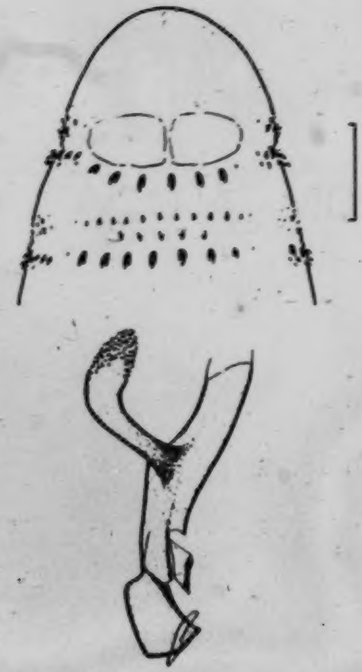
Figures 204 to 207. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 204. *Siphona s.l.*, unplaced, sp. 1 (O162, WSUP).

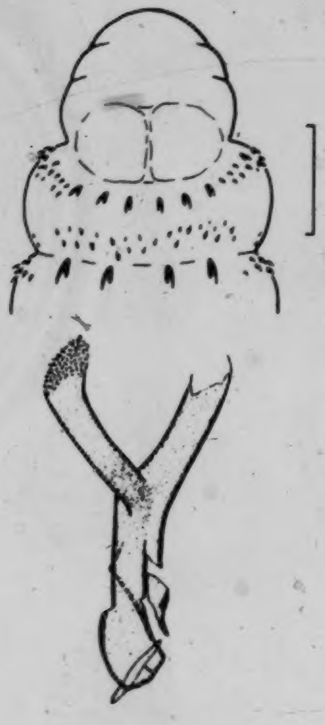
Figure 205. *Siphona s.l.*, unplaced, sp. 2 (O115, CNC).

Figure 206. *Siphona s.l.*, unplaced, sp. 10 (O170, JEOH).

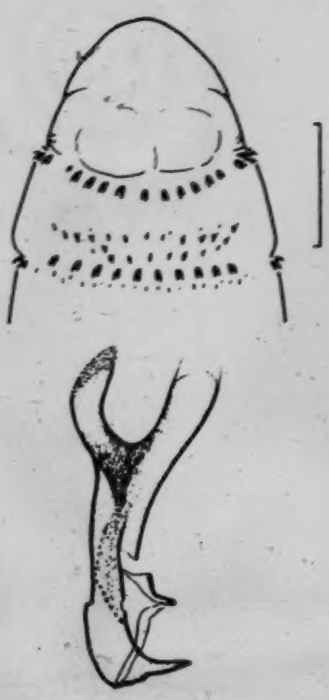
Figure 207. *Siphona s.l.*, unplaced, sp. 14 (R71, CNC).



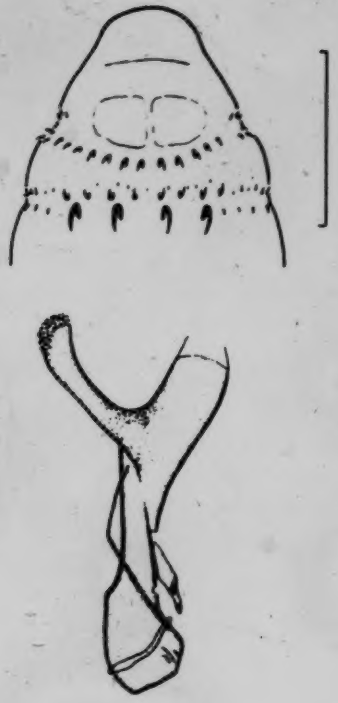
204. *Siphona s.l.*, unplaced, sp. 1



205. *Siphona s.l.*, unplaced, sp. 2



206. *Siphona s.l.*, unplaced, sp. 10

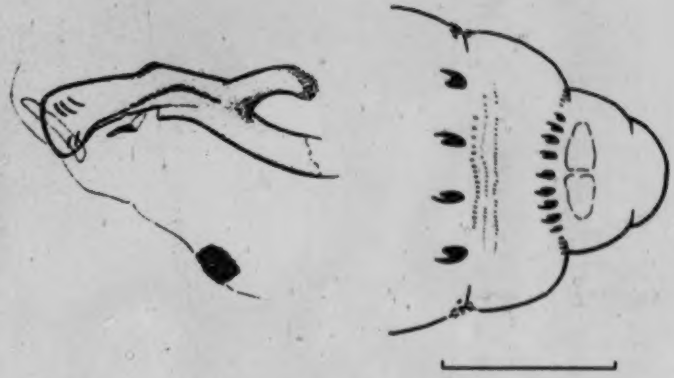


207. *Siphona s.l.*, unplaced, sp. 14

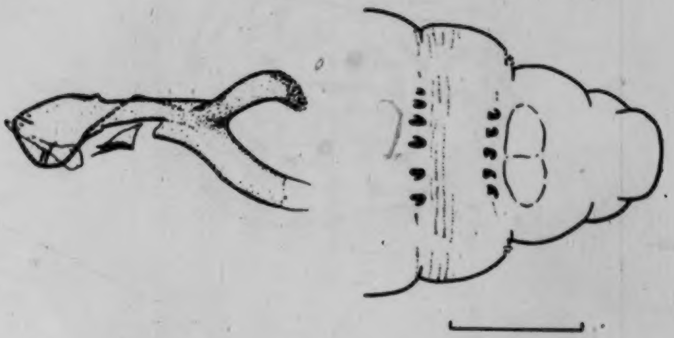
Figures 208 to 209. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 7 to 9 of first instars. Scale bars = 0.05mm.

Figure 208. *Siphona s.l.*, unplaced, sp. 20 (B87, CNC).

Figure 209. *Siphona s.l.*, unplaced, sp. 23 (O22, CNC).



208. *Siphona s.l.*, unplaced, sp. 20



209. *Siphona s.l.*, unplaced, sp. 23

5. HOSTS

5.1 Hosts

Hosts are recorded for over 60 siphonine species, or about 20% of the described fauna, in Table 2. It is difficult to speculate about host preferences from such meagre information, though a few general patterns are suggested by this compilation of host records. Most apparent is that siphonines are primarily parasitoids of larval Lepidoptera, as host species are known from only three families in other orders, the Pyrrhocoridae (Hemiptera), Tenthredinidae (Hymenoptera) and Tipulidae (Diptera).

Within the Lepidoptera there is marked preference for the Macrolepidoptera, with only *Peribaea* and *Actia* known with certainty from hosts in both the Microlepidoptera and Macrolepidoptera. Within the Macrolepidoptera the Geometridae are parasitized by species in the most supraspecific taxa (nine), followed closely by the Noctuidae (seven). *Actia* seems the most generalized siphonine group in terms of host preference, with records from nine families of Microlepidoptera and six families of Macrolepidoptera, though this may in part be attributable to the large number of hosts known for this genus.

A brief section about hosts follows each generic or subgeneric description in the Classification chapter of this work. Because no striking patterns of host preference are evident between siphonine groups, and hosts are still inadequately known, host information is not used in the phylogenetic analysis of the Siphonini.

5.1.1 Explanation of parasite-host list

Table 2 is a compilation of the known hosts of siphonine species. Almost all records have been taken from the literature, though a few are new. New records were obtained from label data and are accompanied in Table 2 by the museum where specimens bearing the listed host data are deposited.

Siphonine species names are listed in bold face and their hosts in italics. The former are listed alphabetically by genus and species and the latter first by family and second by genus and species (thereby grouping together host species belonging to the same family). Siphonine names are those used herein, and an attempt has been made to update host names to correspond with current usage.

The literature includes many host records for tachinids that are unreliable because of questionable species identifications. The records used here are mostly from critically compiled works published by tachinid specialists, and as such are more reliable than the primary literature (though even these authors undoubtedly repeat some published errors because of the paucity of information about most siphonine species).

Where records or species identifications were listed as questionable in a reference cited here, I have preceded the questionable name with a question mark.

Table 2. Parasite-host list for world Siphonini

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Actia crassicornis (Meigen)		
Depressaria applana Fabr.	Oecophoridae	Lundbeck, 1927:461; Herting, 1960:60; Mesnil, 1963a:817
Depressaria astrantiae Heinem.	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Depressaria bupleurella Heinem.	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Depressaria costosa Haworth	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Depressaria depressella Hb.	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Depressaria heydenii Zeller	Oecophoridae	Lundbeck, 1927:461; Herting, 1960:60; Mesnil, 1963a:817
Depressaria hippomarathri Nick.	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Depressaria liturella Schiff.	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Sparganothis pilleriana Sch.	Tortricidae	Herting, 1960:60; Mesnil, 1963a:817
Tortrix viridana L.	Tortricidae	Lundbeck, 1927:461; Herting, 1960:60; Mesnil, 1963a:817
Yponomeuta malinellus Z.	Yponomeutidae	Hubenov, 1985:29
Actia diffidens Curran		
Acleris variana Fernald	Tortricidae	Prebble, 1935; Arnaud, 1978:52
Choristoneura conflictana Walker	Tortricidae	Arnaud, 1978:52
Spilonota ocellana Denis & Schiff.	Tortricidae	Arnaud, 1978:52
Actia eucosmae Bezzi		
Crocidosema plebeiana Zeller	Tortricidae	Crosskey, 1973:176
Actia hargreavesi Curran		
Dysdercus sp. (Hemiptera)	Pyrrhocoridae	Mesnil, 1963a:814 (as *Actia comitata*) (doubtful record)
Actia infantula (Zett.)		
Monopis rusticella Hübner	Tineidae	Herting, 1960:61; Mesnil, 1963a:819
Actia interrupta Curran		
Melanolophia imitata Walker	Geometridae	Arnaud, 1978:53
Schizura concinna Smith	Notodontidae	Arnaud, 1978:53
Acleris variana Fernald	Tortricidae	Arnaud, 1978:53
Acleris variegana Denis & Schiff.	Tortricidae	Arnaud, 1978:53
Amorbia cuneana Walsingham	Tortricidae	Arnaud, 1978:53
Archippus packardianus Fernald	Tortricidae	Arnaud, 1978:53
Archips argyrospilus Walker	Tortricidae	Arnaud, 1978:53
Archips rosanus L.	Tortricidae	Arnaud, 1978:54
Choristoneura conflictana Walker	Tortricidae	Arnaud, 1978:54
Choristoneura fumiferana Clemens	Tortricidae	Arnaud, 1978:54
Choristoneura pinus Freeman	Tortricidae	Arnaud, 1978:54
Choristoneura rosaceana Harris	Tortricidae	Arnaud, 1978:54
Croesia albicomana Clemens	Tortricidae	Arnaud, 1978:54

Table 2. Parasite-host list for world Siphonini (cont.)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Epinotia crenana Hübner	Tortricidae	Arnaud, 1978:53
Epinotia emarginana Walsingham	Tortricidae	Arnaud, 1978:53
Grapholitha molesta Busck	Tortricidae	Arnaud, 1978:53
Phalonia oenotherana Riley	Tortricidae	Arnaud, 1978:54
Xenotemna pallorana Robinson	Tortricidae	Arnaud, 1978:54
Actia near interrupta Curran		
Archips cerasivoranus Fitch	Tortricidae	Arnaud, 1978:55
Archips fervidanus Clemens	Tortricidae	Arnaud, 1978:55
Actia jocularis Mesnil		
Lymantria dispar L.	Lymantriidae	Schaefer & Shima, 1981:370
Actia lamia (Meigen)		
Ourapteryx sambucaria L.	Geometridae	Herting, 1960:60; Mesnil, 1963a:822
Lasiocampa querus L.	Lasiocampidae	Wainwright, 1928:208; Herting, 1960:60; Mesnil, 1963a:822
Epiblema luctuosana Dup.	Tortricidae	Herting, 1960:60; Mesnil, 1963a:822
Epiblema pflugiana Haworth	Tortricidae	Lundbeck, 1927:460; Herting, 1960:60; Mesnil, 1963a:822
Laspeyresia cosmophorana Treitschke	Tortricidae	Mesnil, 1963a:822
Actia maksymovi Mesnil		
Cacoecia murinana Hübner	Tortricidae	Herting, 1960:61; Mesnil, 1963a:823
Semasia diniana Hübner	Tortricidae	Herting, 1960:61; Mesnil, 1963a:823
Spilonota laricīana Hein.	Tortricidae	Herting, 1960:61; Mesnil, 1963a:823
Actia near maksymovi Mesnil		
Dioryctria abietella Denis & Schiff.	Pyralidae	Crosskey, 1976a:291
Actia nigroscutellata Lundbeck		
Elachista megerleella Staint.	Elachistidae	Herting, 1960:61; Mesnil, 1963a:825
Laspeyresia cosmophorana Tr.	Tortricidae	Mesnil, 1963a:825
Laspeyresia servillana Dup.	Tortricidae	Herting, 1960:61 (as questionable); Mesnil, 1963a:825
Olethreutes roseomaculana Herr.-Sch.		
or *Olethreutes dalecarliana* Guenée	Tortricidae	Lundbeck, 1927:463; Herting, 1960:61; Mesnil, 1963a:825
Semasia ustomaculana Curtis	Tortricidae	Lundbeck, 1927:463; Herting, 1960:61; Mesnil, 1963a:825
Tortrix viridana L.	Tortricidae	Hubenov, 1985:29
Actia nudibasis Stein		
Heringia dodecella L.	Gelechiidae	Herting, 1960:60; Mesnil, 1963a:826
Dioryctria splendidella Herr.-Sch.	Pyralidae	Herting, 1960:60; Mesnil, 1963a:826; Shima, 1970c:187
Evetria buoliana Schiff.	Tortricidae	Lundbeck, 1927:459; Herting, 1960:61; Mesnil, 1963a:826

Table 2. Parasite-host list for world Siphonini (cont.)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Evetria resinella L.	Tortricidae	Lundbeck, 1927:459; Herting, 1960:60; Mesnil, 1963a:826
Actia painei Crosskey		
Agonoxena pyrogramma Meyrick	Agonoxenidae	Crosskey, 1962:175
Actia pamirica Richter		
Parapandemis chondrillana H. S.	—	Richter, 1974:1269
Spilonota ocellana F.	Tortricidae	Richter, 1974:1269
Actia parviseta Malloch		
Isotenes miserana Walker	Tortricidae	Crosskey, 1973:176
Actia pilipennis (Fallén)		
Platyptilia rhododactyla Schiff.	Pterophoridae	Herting, 1960:59
Acalla aspersana Hübner	Tortricidae	Herting, 1960:59; ~~Mesnil, 1963a:828~~
Acalla hastiana L.	Tortricidae	Mesnil, 1963a:828
Acalla logiana Schiff.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Ancylis mitterbacheriana Schiff.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Ancylis tineana Hübner	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Capua angustiorana Haworth	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Eucosma sordidana Hübner	Tortricidae	Mesnil, 1963a:828
Olethreutes schulziana Fabr.	Tortricidae	Mesnil, 1963a:828
Sparganothis pilleriana Schiff.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Tortrix bergmanniana L.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Tortrix loefflingiana L.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828; Hubenov, 1985:29
Tortrix pronubana Hübner	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Tortrix viridana L.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828; Hubenov, 1985:29
Actia spp. (North America)		
Phyganidia californica Packard	Dioptidae	Arnaud, 1978:56
Gnorimoschema spp.	Gelechiidae	Arnaud, 1978:56
Catocala relicta Walker	Noctuidae	Arnaud, 1978:56
Heterocampa guttivitta Walker	Notodontidae	Arnaud, 1978:56
Epinotia similana Hübner	Tortricidae	Arnaud, 1978:56
Episimus argutanus Clemens	Tortricidae	Arnaud, 1978:56
Actia spp. (Old World)		
Gaesa bisignella Snellen	Gelechiidae	Crosskey, 1976a:291
Herpetogramma licarsisalis Walker	Pyralidae	Cantrell, 1986:259
Epiphyas postvittana Walker	Tortricidae	Cantrell, 1986:259

Table 2. Parasite-host list for world Siphonini (cont.)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Ceromya americana (Townsend)		
Schizura concinna Smith	Notodontidae	Arnaud, 1978:51
Ceromya apicipunctata (Malloch)		
Unidentified sp.	Noctuidae	Crosskey, 1976a:291
Ceromya bicolor (Meigen)		
Phragmatobia fuliginosa L.	Arctiidae	Herting, 1960:61; Mesnil, 1963a:835
Dendrolimus pini L.	Lasiocampidae	Herting, 1960:61; Mesnil, 1963a:835
Eriogaster lanestris L.	Lasiocampidae	Lundbeck, 1927:466; Herting, 1960:61; Mesnil, 1963a:835
Gastropacha quercifolia L.	Lasiocampidae	Herting, 1960:61; Mesnil, 1963a:835
Lasiocampa quercus L.	Lasiocampidae	Lundbeck, 1927:466; Herting, 1960:61; Mesnil, 1963a:835
Dolerus pratensis L. (Hymenoptera)	Tenthredinidae	Mesnil, 1963a:835
Ceromya cibdela (Villeneuve)		
Stylochilus sp.	Sphingidae	New record (CNC)
Ceromya ?hermanni (Bezzi)		
Unidentified sp.	Geometridae	Crosskey, 1973:176
Ceromya luteicornis (Curran)		
Unidentified sp.	Saturniidae	Curran, 1933c:162
Nudaurelia belina	—	Curran, 1933c:162
Ceromya ontario (Curran)		
Ennomos subsignarius Hübner	Geometridae	Arnaud, 1978:55
Ceromya palloris (Coquillett)		
Drepana arcuata Walker	Drepanidae	Arnaud, 1978:55
Drepana bilineata Packard	Drepanidae	Arnaud, 1978:55
Ceromya near palloris (Coquillett)		
Ennomos subsignarius Hübner	Geometridae	Arnaud, 1978:55
Eugonobapta nivosaria Guenée	Geometridae	Arnaud, 1978:55
Ceromya patellicornis Mesnil		
Callopistria repleta Walker	Noctuidae	Crosskey, 1976a:291
Ceromya pruinosa Shima		
Dendrolimus undans flaveola Motsch.	Lasiocampidae	Shima, 1973:155

Table 2. Parasite-host list for world Siphonini (cont.)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Ceromya silacea (Meigen)		
Erastria fasciana L.	Noctuidae	Herting, 1960:61; Mesnil, 1963a:839
Ceromya spp. (Australia)		
Ectropis excursaria Guenée	Geometridae	Cantrell, 1986:259
Chrysodeixis argentifera Guenée	Noctuidae	Cantrell, 1986:259
Euplexia nigerrima Guenée	Noctuidae	Cantrell, 1986:259
Homoeosoma vagella Zeller	Pyralidae	Cantrell, 1986:259
Goniocera io (Aldrich)		
Malacosoma americanum Fab.	Lasiocampidae	Arnaud, 1978:126
Malacosoma disstria Hübner	Lasiocampidae	Arnaud, 1978:126
Goniocera schistacea (B.B.)		
Malacosoma castrensis L.	Lasiocampidae	Herting, 1960:119; Mesnil, 1963:801
Goniocera versicolor (Fallén)		
Malacosoma neustria L.	Lasiocampidae	Herting, 1960:120; Mesnil, 1963:803
Peribaea aegyptia (Villeneuve)		
Acantholeucania loreyi Dup.	Noctuidae	Crosskey, 1973:176
Aedia leucomelas	Noctuidae	Shima, 1981:450
"*Cirphis*" sp.	Noctuidae	Crosskey, 1976a:291
Earias sp(p).	Noctuidae	Mesnil, 1963a:806
Heliothis armigera Hübner	Noctuidae	Shima, 1981:450; Crosskey, 1976a:291
Heliothis sp.	Noctuidae	Crosskey, 1973:176
Laphygma sp(p).	Noctuidae	Mesnil, 1963a:806
Leucania separata	Noctuidae	Shima, 1981:450
Leucania venalba Moore	Noctuidae	Shima, 1981:450; Crosskey, 1976a:291
Platysenta dolorosa Walker	Noctuidae	Cantrell, 1986:259
Prodenia sp(p).	Noctuidae	Mesnil, 1963a:806
Pseudaletia unipuncta Haworth	Noctuidae	Shima, 1981:450; Crosskey, 1973:176 & 1976a:291
Spodoptera exempta Walker	Noctuidae	Crosskey, 1973:176
Spodoptera exigua Hübner	Noctuidae	Shima, 1981:450; Crosskey, 1976a:291
Spodoptera littoralis Boisd.	Noctuidae	Kugler, 1979:56
Spodoptera litura Fabr.	Noctuidae	Shima, 1981:450; Crosskey, 1973:176 & 1976a:291 and Jayanth & Nagarkatti 1984:77
Spodoptera mauritia Boisd.	Noctuidae	Shima, 1981:450; Crosskey, 1976a:291
Spodoptera sp(p).	Noctuidae	Mesnil, 1963a:806
Hedylepta indicata	Pyralidae	Shima, 1981:450

Table 2. Parasite-host list for world Siphonini (cont.)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Peribaea argentifrons (Malloch)		
Copromorpha prasinochroa Meyrick	Copromorphidae	Crosskey, 1973:176
Homoeosoma vagella Zeller	Pyralidae	Crosskey, 1973:176
Peribaea fissicornis (Strobl)		
Angerona prunaria L.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Boarmia bistortata Goeze	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Boarmia consortaria Fabr.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Bupalus piniarius L.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Himera pennaria L.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Ourapteryx sambucaria L.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Phigalia pedaria Fabr.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Poecilocampa populi L.	Lasiocampidae	Herting, 1960:59; Mesnil, 1963a:807
Peribaea hyalinata (Malloch)		
Hyblaea puera Cramer	Hyblaeidae	Crosskey, 1976a:291
Pyrausta machoeralis Walker	Pyralidae	Crosskey, 1976a:291
Peribaea palaestina (Villeneuve)		
Spodoptera exigua Hübner	Noctuidae	Kugler, 1979:56
Spodoptera littoralis Boisd.	Noctuidae	Kugler, 1979:56
Peribaea plebeia (Malloch)		
Earias huegeli Rogenhofer	Noctuidae	Crosskey, 1973:176
Peribaea sp. ? plebeia (Malloch)		
? *Anthela* sp.	Anthelidae	Crosskey, 1973:176
Peribaea stiglina (Bezzi)		
Stiglina superior Butl.	Thyrididae	Bezzi, 1928:204
Peribaea suspecta (Malloch)		
Earias vittella Fabr.	Noctuidae	Crosskey, 1976a:291
Earias sp.	Noctuidae	Curran, 1928:237; Crosskey, 1976a:291
Peribaea tibialis (Robineau-Desvoidy)		
Ennomos autumnaria Wornb.	Geometridae	Hubenov, 1985:29
Ennomos quercinaria Hufn.	Geometridae	Hubenov, 1985:29
Prosopolopha jourdanaria Vill.	Geometridae	Herting, 1960:59; Mesnil, 1963a:813
Lasiocampa grandis Stgr.	Lasiocampidae	Herting, 1960:59; Mesnil, 1963a:813; Kugler, 1979:56
Orgyia dubia Tausch.	Lymantriidae	Herting, 1960:59; Mesnil, 1963a:813; Kugler, 1979:55

Table 2. Parasite-host list for world Siphonini (cont.)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Anarta myrtilli L.	Noctuidae	Herting, 1960:59; Mesnil, 1963a:813
Asticta pastinum Tr.	Noctuidae	Mesnil, 1963a:813
Spodoptera exigua Hübner	Noctuidae	Kugler, 1979:56
Yponomeuta malinellus Z.	Yponomeutidae	Hubenov, 1985:29
Perihaea sp. (Australia)		
Spodoptera exigua Hübner	Noctuidae	Cantrell, 1986:259
Crocidosema plebejana Zeller	Tortricidae	Cantrell, 1986:259
S. (Aphantorhaphopsis) mallochiana (Gardner)		
Pelopidas mathias Fabr.	Hesperiidae	Crosskey, 1976a:291
"Turmeric skipper"	Hesperiidae	Crosskey, 1976a:291
"Ginger lily leaf-roller"	Hesperiidae	Crosskey, 1976a:291
"Rice leaf-roller skipper"	Hesperiidae	Crosskey, 1976a:291
S. (Aphantorhaphopsis) norma (Malloch)		
Pseudaletia convecta	Noctuidae	Crosskey, 1973:176
S. (Aphantorhaphopsis) samarensis (Vill.)		
Porthetria dispar L.	Lymantriidae	New record (USNM)
S. (Aphantorhaphopsis) selecta (Pand.)		
Paidia murina Hübner	Arctiidae	Herting, 1978:7
S. (Aphantorhaphopsis) siphonoides (Strobl)		
Deilinia pusaria L.	Geometridae	Herting, 1960:62; Mesnil, 1964: 850
Xanthorhoe biriviata Borkh.	Geometridae	Herting, 1960:62; Mesnil, 1964: 850
S. (Baeomyia) juniperi O'Hara		
Semiothisa trivata B. & McD.	Geometridae	O'Hara, 1984:1395
S. (Baeomyia) xanthogaster O'Hara		
Semiothisa sexmaculata Packard	Geometridae	O'Hara, 1984:1395
Semiothisa spp.	Geometridae	O'Hara, 1984:1395
Unidentified spp.	Geometridae	O'Hara, 1984:1395
S. (Ceranthia) abdominalis (R.-D.)		
Cosymbia annulata Schultze	Geometridae	Herting, 1960:62; Mesnil, 1963a: 841
Cosymbia orbicularia Hübner	Geometridae	Herting, 1960:62 & 1966:6; Mesnil, 1963a: 841
Cosymbia pendularia Cl.	Geometridae	Herting, 1966:6
Cosymbia porata F.	Geometridae	Herting, 1960:62 & 1966:6; Mesnil, 1963a: 841

Table 2. Parasite-host list for world Siphonini (cont.)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Cosymbia ruficiliaria H.S.	Geometridae	Herting, 1966:6
S. (Ceranthia) lichtwardtiana (Villeneuve)		
Acasis viretata Hübner	Geometridae	Herting, 1966:6
S. (Ceranthia) pallida (Herting)		
Eupithecia denotata Hübner	Geometridae	Herting, 1960:62; Mesnil, 1963a: 843
S. (Ceranthia) tristella Herting		
Eupithecia silenata Standf.	Geometridae	Herting, 1966:6
Eupithecia undata Frr.	Geometridae	Herting, 1966:6
S. (Pseudosiphona) brevirostris (Coquillett)		
Oidaematophorus homodactylus Walker	Pterophoridae	Arnaud, 1978:452 (doubtful record)
S. (Pseudosiphona) spp.		
Chloropteryx sp.	Geometridae	New record (USNM)
Unidentified sp.	Lycaenidae	New record (USNM)
S. (Siphona) collini Mesnil		
Cerapteryx graminis L.	Noctuidae	Andersen, 1982:157
Euxoa temera Hübner	Noctuidae	Andersen, 1982:157
Euxoa tritici L.	Noctuidae	Andersen, 1982:157
S. (Siphona) confusa Mesnil		
Mythimna littoralis Curtis	Noctuidae	Andersen, 1982:157
Phlogophora meticulosa L.	Noctuidae	Andersen, 1982:157
S. (Siphona) geniculata (De Geer)		
Anticollix sparsata Treitschke	Geometridae	Andersen, 1982:157
Erannis defoliaria Clerck	Geometridae	Andersen, 1982:157
Antitype chi L.	Noctuidae	Andersen, 1982:157
Caradrina morpheus Hufnagel	Noctuidae	Andersen, 1982:157
Hadena bicruris Hufnagel	Noctuidae	Andersen, 1982:157
Lacanobia suasa Denis & Schiff.	Noctuidae	Andersen, 1982:157
Lacanobia oleracea L.	Noctuidae	Andersen, 1982:157
Mamestra brassicae L.	Noctuidae	Andersen, 1982:157
?*Mythimna ferrago* Fabr.	Noctuidae	Andersen, 1982:157
?*Mythimna littoralis* Curtis	Noctuidae	Andersen, 1982:157
?*Mythimna obsoleta* Hübner	Noctuidae	Andersen, 1982:157
?*Phlogophora meticulosa* L.	Noctuidae	Andersen, 1982:157

Table 2. Parasite-host list for world Siphonini (cont.)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Smerinthus ocellata L.	Sphingidae	Andersen, 1982:157
S. (Siphona) maculata Staeger		
Euxoa obelisca Denis & Schiff.	Noctuidae	Andersen, 1982:157
Ochropleura candelisequa Denis & Schiff.	Noctuidae	Andersen, 1982:157
S. (Siphona) minuta (Fabr.)		
Ceramica pisi L.	Noctuidae	Andersen, 1982:158 (doubtful record)
Tipula fulvipennis De Geer	Tipulidae	Andersen, 1982:158
Tipula lateralis Meigen	Tipulidae	Andersen, 1982:157
Tipula maxima Poda	Tipulidae	Andersen, 1982:158
Tipula montium Egger	Tipulidae	Andersen, 1982:157
Tipula oleracea L.	Tipulidae	Andersen, 1982:157
Tipula paludosa Meigen	Tipulidae	Andersen, 1982:157
Tipula subnodicornis Zett.	Tipulidae	Andersen, 1982:157
Tipula vittata Meigen	Tipulidae	Andersen, 1982:158
S. (Siphona) nigricans (Villeneuve)		
Tipula irrorata Macquart	Tipulidae	Herting, 1967a:9; Andersen, 1982:158
S. (Siphona) pseudomaculata Blanchard		
Faronta albilinea Hübner	Noctuidae	Blanchard, 1963:252; Guimarães, 1977:74
S. (Siphona) setosa Mesnil		
Eupithecia succenturiata L.	Geometridae	Andersen, 1982:157
Allophyes oxyacantae L.	Noctuidae	Andersen, 1982:157
S. (Siphonopsis) brasiliensis Townsend		
Rachiplusia nu Guenée	Noctuidae	Guimarães, 1977:74
Syngrapha gammoides Blanchard	Noctuidae	Guimarães, 1977:74
S. (Siphonopsis) conata Reinhard		
Phryganidia californica Packard	Dioptidae	Arnaud, 1978:458
S. (Siphonopsis) plusiae (Coquillett)		
Phryganidia californica Packard	Dioptidae	Arnaud, 1978:458
Autographa californica Speyer	Noctuidae	Arnaud, 1978:459
Trichoplusia ni Hübner	Noctuidae	Arnaud, 1978:459
Unidentified spp.	Noctuidae	Arnaud, 1978:459
Siphona s. l. (New World) sp. 7		

Table 2. Parasite-host list for world Siphonini (cont.)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Cladara limitaria Walker	Geometridae	New record (CNC)
Stenoporpia sp.	Geometridae	New record (CNC)
Panthea portlandia Grt.	Noctuidae	New record (CNC)
Siphona s. l. (New World) sp. 8		
Ectropis crepuscularia Denis & Schiff.	Geometridae	New record (CNC)
Epirrita autumnata Bkh.	Geometridae	New record (CNC)
Melanolophia imitata Walker	Geometridae	New record (CNC)

6. EVOLUTION OF THE SIPHONINI

6.1 Introduction

Many methods are presently available for inferring phylogenies through cladistic analyses, but all are theoretically similar in that they begin with polarization of character states into plesiotypic (ancestral) and apotypic (derived), generally in conjunction with an outgroup comparison. Taxa are then ordered into a hierarchy of nested sets (a cladogram) on the basis of synapotypic (shared derived) states. General methods of phylogenetic analysis are described by Wiley (1981) and are under constant review and refinement in the pages of *Systematic Zoology*.

Polarization of character states in the Siphonini is not possible for many of the characters given in the Structural Features chapter. One of the problems is the uncertainty regarding the sister group to the Siphonini. This problem required that the outgroup comprise a selection of species from several tachinid tribes of possible close relationship to the Siphonini. Names of species selected for this purpose are listed in Table 3 along with their geographic distribution. Such an extended outgroup was useful for detecting and dismissing many very homoplastic states from the phylogenetic analysis, but also required the rejection of possibly useful states which might have been phylogenetically interpretable if tribal relationships between the Siphonini and the extended outgroup were better resolved. A preliminary analysis of the phylogenetics of the Siphonini established *Siphona s.l.* as a higher clade within the tribe, so non-*Siphona s.l.* siphonines were considered the functional outgroup (Watrous and Wheeler 1981) for polarization of states among *Siphona s.l.* subgenera.

Character weighting is a controversial subject because any system of weighting is relatively subjective in practice, yet equal weighting of all apotypic states is even more undesirable because a simple tally of apotypic states does not recognize the fundamental value of evolutionary novelty and complexity in phylogenetic reconstruction.

A very simple approach to character weighting has been adopted here. Two levels of synapotypy are recognized - primary and secondary. A primary synapotypy is one founded on state complexity and a minimum of homoplasy within both outgroup and the Siphonini. A secondary synapotypy is usually structurally less complex and/or more homoplastic than a primary synapotypy, or the character has been insufficiently studied for the apotypic state to be hypothesized as a primary synapotypy at this time.

Primary and secondary synapotypies of the Siphonini provide good evidence for the monophyly of most siphonine genera and subgenera but resolve few intergeneric, or *Siphona s.l.* intersubgeneric, relationships (Fig. 210).

The synapotypies for siphonine genera and subgenera are discussed under the Phylogenetics section of each taxon in the Classification chapter. They are summarized below and designated as primary or secondary, and incidents of homoplasy are noted. Many characters of the Structural Features chapter are deemed unsuitable for phylogenetic analysis so the numbers below do not correspond to those in that chapter. Similarly, certain states are defined differently below than in the Structural Features chapter so a direct correlation is not possible between the states in both sections. Characters and states of the Structural Features chapter that are the same as those discussed here are indicated below in square brackets. The three species groups of undescribed *Siphona s.l.* are considered inadequately studied to include under the discussion of primary and secondary synapotypies.

Intergeneric relationships of non-*Siphona s.l.* siphonines and intersubgeneric relationships of *Siphona s.l.* are not interpretable by primary or secondary synapotypies except for the *Proceromyia-Entomophaga* lineage. However, the distribution of certain, less-reliable, states suggest possible higher relationships within these groups, and these possibilities are explored at the end of this section and depicted in Figs. 212-217.

Table 3. Tachinid species examined for outgroup comparison with the Siphonini.

TRIBE AND SPECIES	DISTRIBUTION
Ernestiini	
Eloceria delecta (Meigen)	Europe
Synactia parvula (Rondani)	Europe
Triarthriini	
Triarthria setipennis (Fallén)	Europe
Aphriini	
Aphria ocypterata Townsend	Nearctic
Solieria pacifica (Meigen)	western Palearctic
Solieria sp.	Arizona (USA)
Leskiini	
Atylostoma towadensis (Matsumura)	eastern Palearctic & SE Asia
Drepanoglossa lucens Townsend	Nearctic
Genea brevirostris (James)	eastern Nearctic
Genea texensis (Townsend)	Nearctic
Genea robertsonii (Townsend)	southern Nearctic
Leskia aurea (Fallén)	Palearctic
Leskia depilis (Coquillett)	eastern Nearctic
Leskia sp.	New Mexico (USA)
Trochiloleskia loriola (Reinhard)	southern Nearctic
Clausicellini	
Clausicella sp.	Arizona (USA)
Crocinosoma cornuale Reinhard	southern Nearctic
Dolichopalpellus mirabilis Townsend	SE Brazil
Epicoronimyia mundelli (Blanchard)	Argentina & Chile
Ginglymia acirostris Townsend	Nearctic
Ginglymia johnsoni (Coquillett)	Nearctic
Phantasiomyia sp.	California (USA)
Spathipalpus philippi Rondani	Argentina & Chile
Neaerini	
Camposodes evanescens Cortés	Chile
Neaera laticornis (Meigen)	Palearctic
Neaera leucoptera (Johnson)	central and eastern Nearctic
Neaera robertsonii (Townsend)	central and eastern Nearctic
Phytomyptera setigera (Thomson)	western Nearctic
Phytomyptera sp.	Arizona (USA)

6.2 Monophyly of the Siphonini

1P. The best supported synapotypy of the Siphonini is the presence of only two spermathecae in the reproductive system of adult females. This synapotypy was proposed by Andersen (1983) in his revision of the Old World Siphonini, and is supported here by its universality among all female siphonines dissected during this study (comprising approximately 90 species, or almost 25% of the known described and undescribed siphonine species). Only species of the unrelated Neotropical genus *Phaenopsis* Townsend are known to share this state within the Tachinidae (Andersen 1983).

2P. The pregonite of adult male siphonines is membranous anteriorly from its apex to its basal articulation with the hypandrium (Figs. 71-106; universal among dissected males of over 250 siphonine species). According to Tschorsnig (1985 and pers. comm.), this state is unique to the Siphonini, with other tachinids lacking membrane in this position. Based on Tschorsnig's findings the state in the Siphonini is tentatively proposed as a synapotypy of the tribe.

3S. Possibly synapotypic of the Siphonini is absence of accessory glands from the reproductive system of adult males. This synapotypy was suggested by Andersen (1983), based on examination of dissected males of a limited number of Old World siphonine species. Andersen noted that male accessory glands are absent from several other, apparently unrelated, tachinids. This synapotypy is in need of corroboration because it is based on few representatives of the Siphonini and was not investigated during this study.

Andersen (1983) also proposed that convergent subapical setae on the scutellum are synapotypic of the Siphonini. This state is shared with possible sister groups to the Siphonini (in particular some species of the Leskiini and Clausicellini) and therefore cannot be defended as synapotypic of the tribe at this time.

6.3 Monophyly of genera and subgenera

Goniocera Brauer and Bergenstamm

4P. *Goniocera* species are unique among siphonines in having a row of *ad* setae on the mid tibia. This state is shared with few species in the outgroup, but most outgroup species have one seta in this position. This latter state is probably in the groundplan of both the outgroup and the Siphonini. [Character 24.]

5P. Known hosts are larvae of *Malacosoma* species (tent caterpillars), a parasitic habit unique to this genus (host of *G. montium* unknown).

6S. Median lobe of male sternum 5 prominent and flattened on posteromedial surface (Fig. 47; *G. montium* not examined). This state is approached in few other siphonines and similar in few *Ceromya s.s.* species, but is probably independently derived in *Goniocera*. [Character 40, state F.]

7S. Posterolateral margin of distiphallus curved inward toward midline and slightly incised from rest of lateral surface (not visible in Fig. 107 and not examined in *G. montium*). This state is only known to be shared with *Ceromya flaviseta* and *C. ontario*, but other characters do not support a close relationship between these species. [Character 49, state S.]

8S. Female sternum 8 reduced in size (Fig. 145). This state is not considered a primary synapotypy because the female genitalia of two of the four species, *G. montium* and *G. versicolor*, were not examined. [Character 62, state R.]

9S. Male surstylus narrowly fused basally with the epandrium (Fig. 137, not examined in *G. montium*). This state is common in many *Ceromya* species but few other siphonines, so may be independently derived in *Goniocera*. [Character 52, state F.]

10S. Male cerci sharply inflexed at midpoint and densely setose on basal half (Fig. 137, not examined in *G. montium*). Like the former character, this condition of the cerci in *Goniocera* species is shared with many *Ceromya* species and few other siphonines. [In part, character 54, state I.]

Proceromyia Mesnil

11P. Distiphallus in lateral view with long, broad, anteriorly spined, anterolateral arm and short lateral projection (Figs. 108-109). Shape of the distiphallus is closely approximated only in the hypothesized sister group, *Entomophaga* (Figs. 110-111).

12P. Male sternum 5 (Figs. 48-49) with apical lobe slightly differentiated [character 38, state O] and median lobe slightly sinuous and rounded [character 40, state R].

13P. Head with narrow vertex (Mesnil and Shima 1978: 325).

14P. Large tarsal claws. This state is also present in few *Siphona s.s.* species, though certainly independently evolved in that group. [Character 26, state L.]

15S. A possible synapotypy is the bare prosternum. This state is shared with *Ceromya monstrosicornis*, some specimens of *Goniocera io* and few other siphonines. Setulation on the prosternum is a difficult character to polarize because it is obviously very homoplastic. A bare prosternum predominates in the outgroup, but some species of the Clausicellini and Neaerini have a setulose prosternum. The latter state is almost universal among siphonines, but particularly for two reasons - its presence in *Entomophaga* (the hypothesized sister group to *Proceromyia*), and its requirement of fewer reversals - a setulose prosternum is here considered the more likely groundplan state of the Siphonini.

Entomophaga Lioy

16P. Aristomere 1 elongate, at least 1.5X longer than wide (Figs. 4-5). This state is also autapotypic of few *Siphona s.l.* species. [Character 9, state L.]

17S. The general habitus of the two *Entomophaga* species, particularly with respect to head features (Figs. 4-5; small eye, similar-shaped flagellomere 1) suggests they are sister species.

18S. Female sternum 8 is absent from *E. nigrohalterata* (Fig. 147). If similarly absent from the female of *E. exoleta*, then this condition would represent a primary synapotypy.

Ceromya s.l. Robineau-Desvoidy

19S. It is not possible to cite a single state which is synapotypic of *Ceromya s.l.* species, yet *Ceromya s.s.* and the *C. silacea* species group are probably each monophyletic and have certain features in common which attest to their close evolutionary grade if not strict monophyly. These include the diagnostic features of *Ceromya s.l.* given in the Classification chapter as well as the following features of the male genitalia shared by some but not all species of both subgroups (and few other siphonines, most notably *Goniocera* species (Fig. 137), the significance of which is discussed later in this chapter): surstylus basally fused with epandrium [character 52, state F], cerci sharply inflexed at midpoint [character 54, state I] and densely setose on basal half (Fig. 138). All the above states are grouped together here as a secondary synapotypy of *Ceromya s.l.* because they may be phylogenetically important even though they do not clearly establish the monophyly of the genus.

Andersen (1983) proposed as a synapotypy of *Ceromya s.l.*: "Praegonite oval with the sclerotized part more or less bilobed and recurved" (p. 12). Shape of the sclerotized portion of the pregonite is more varied than suggested by Andersen and is therefore not considered a synapotypy here. However, the oval shape is attributable to the enlarged membrane anteriorly, and this is here considered a synapotypy of *Ceromya s.s.*

Ceromyia s.s. Robineau-Desvoidy

20P. Features of the pregonite provide the only convincing synapotypy of this group. The membrane anteriorly on the pregonite is characteristically enlarged and in most species spinulose (Figs. 39-40, 77-83). (The spinules are very tiny in some species and consequently have been overlooked by previous workers.) Almost all *Ceromya s.s.* species examined and lacking spinules on the pregonite are assignable to species groups which possess them, so this state is considered that of the groundplan of *Ceromya s.s.* The phylogenetic significance of similar spinules on the pregonite of *Goniocera io* is discussed later in this chapter. [Character 45, state M.]

Ceromya Nepal sp. 1 and *C. monstrosicornis* are tentatively included in *Ceromya s.s.* until their phylogenetic position is better resolved (see Phylogenetics section of *Ceromya s.s.*).

Ceromya silacea species group

21P. Distiphallus with internal sclerotized structure, which is continuous with infolded posterior margins (Fig. 112). This structure is unique to members of the *C. silacea* species group.

22S. The first instar of *C. silacea* has a hook-like labrum (Fig. 160). This is proposed only tentatively because first instars of other members of this group have not been examined.

The phylogenetic history of *Ceromya s.l.* is not clearly understood. The present division of the genus into *Ceromya s.s.* and the *C. silacea* species group is based on male genitalic states, and may be incomplete until males of all described *Ceromya* species are examined. It seems premature to erect a new subgenus for the *C. silacea* species group until the phylogenetics of the genus are better understood. Recognition of two subgenera must await corroboration of *Ceromya s.s.* and the *C. silacea* species group as monophyletic lineages and sister groups.

Actia Robineau-Desvoidy

23P. Male pregonite (Figs. 41-42, 85-86) approximately J-shaped [character 44, state J] and spinose [character 45, state S].

24P. *Actia* species, with few exceptions, possess a row of hairs on the katepisternum anterior to the mid coxa (Fig. 33). This state is unique to *Actia* species and *Entomophaga exoleta* among siphonines, though is also present in some species of the outgroup. No evidence suggests that *Actia* is the primitive lineage of the Siphonini so presence of a katepisternal row of hairs is hypothesized as synapotypic of *Actia* species. The same state in *E. exoleta* is hypothesized as independently derived. [Character 20, state S.]

25P. An approximately V-shaped sternum 5 with an indistinct median lobe (Figs. 58-59) is apparently the groundplan state of the genus and approximated by few other siphonines. [Character 38, state V and character 40, state U.]

26S. Almost all *Actia* species have two setulae on the upper portion of the anepisternum (Fig. 31), whereas one setula is found in most other siphonines (Fig. 32) and is almost universal in the outgroup. This state is weighted as a secondary synapotypy because it is widely distributed throughout different siphonine lineages even though present in relatively few non-*Actia* species. [Character 19.]

27S. The lack of a dorsal cornu in the cephalopharyngeal skeleton of first instars of examined *Actia* species is certainly apotypic (Figs. 168-171), but the universality of this state throughout the genus needs to be investigated. [Character 65, state A.]

Peribaea **Robineau-Desvoidy**

28P. A strong, downwardly directed, proepimeral seta (Fig. 27) is shared by all known *Peribaea* species and absent from other siphonines. Most neaerines and some other tachinids also share this state, but are not closely related to *Peribaea*. [Character 18, state P.]

29P. Distiphallus sclerotized posteriorly (partially unsclerotized [incised] in all but three other examined and unrelated siphonine species). Andersen (1983) considered *Peribaea* to be the most primitive lineage of the Siphonini and a posteriorly sclerotized distiphallus both plesiotypic and the groundplan state in the tribe. My outgroup comparison does not support this polarization (*i.e.* nothing comparable to the *Peribaea* condition was found in the outgroup) and I place *Peribaea* near *Siphona* based on characters discussed below. [Character 48, state E.]

30P. Females of most *Peribaea* species have a distinct sternum 8, though bare as compared with haired as in other siphonines. The female ovipositor is elongate and sternum 8 lacking in few highly derived *Peribaea* species. [Character 62, state B.]

31S. First instars with narrowed, and in most species hook-like, labrum (Figs. 172-175). Outgroup comparison is not helpful in the polarization of this state because both a hook-like and hatchet-like labrum are widely distributed throughout the Tachinidae. Andersen (1983) interpreted *Peribaea* as primitive and a hook-like labrum as plesiotypic, but this state is more likely apotypic if the present phylogenetic placement of *Peribaea* is correct. [Character 64, state N.]

Siphona s.l. Meigen

32P. First instars with from two to a row of large spinules or hooks on the posteroventral margin of segment 7 (Figs. 176-179, 181-209), with the exception of *S. (Aphantorhaphopsis)* Uganda sp. 1 (Fig. 180). Except for *Ceromya* Australia sp. 3 (Fig. 164), non-*Siphona* species have tiny spinules or are bare in this position (Figs. 157-163, 165-175). [Character 66.]

33P. First instars, with few exceptions, with single dominant row of spinules on the posteroventral margin of segment 8. Almost all examined first instars of non-*Siphona* species have two or more rows of spinules or spines in this position [Character 67, state S; refer to figure numbers cited therein.]

The Old World component of *Siphona s.l.*, comprising the subgenera *Aphantorhaphopsis*, *Ceranthia* and *Siphona*, was interpreted as monophyletic by Andersen (1983) based on two hypothesized synapotypies. One was presence of an anterior apodeme on female sternum 7, which is correctly polarized as apotypic in the Siphonini based on outgroup comparison. However, as shown in Table 1 this state is widely distributed throughout the tribe and therefore too homoplastic to interpret as a synapotypy of *Siphona s.l.* [character 58, state W]. The second state that Andersen considered synapotypic of Old World *Siphona s.l.* was presence of a long lower katepisternal seta. I interpret this state differently from Andersen, as discussed under the section on monophyly of *Peribaea* and *Siphona s.l.*

Siphona (Actinocrocuta Townsend)

34S. Pregonite (Fig. 89) very slender and elongate [character 44, state A], with outer surface short spinose apically [character 45, state T].

35S. Distiphallus slender and parallel-sided (Figs. 122-123).

36S. Cerci in posterior view broadened to near apex (Fig. 142).

The above states are individually present in few other siphonines but the combination of all three is unique to this subgenus and none appear to be synapotypic between *S. (Actinocrocuta)* and another *Siphona* subgenus.

Siphona (Aphantorhapha Townsend)

37S. Distiphallus tapered to a rounded or pointed tip (Fig. 124).

38S. Cerci broadened at midlength in posterior view (Fig. 143). The cerci of *S. (Aphantorhapha) atoma* do not share this apotypy and may be plesiotypic in this respect, though other states support a sister group relationship between this species and *S. (Aphantorhapha) arizonica*.

Siphona (Aphantorhaphopsis Townsend)

This taxon is non-monophyletic and comprises all Old World *Siphona s.l.* species not assignable to *S. (Siphona)* or *S. (Ceranthia)*. The included species are too inadequately known to be reclassified into monophyletic lineages at this time. None of the examined species appears to belong in the otherwise strictly New World supraspecific taxa of *Siphona s.l.*

Siphona (Baeomyia O'Hara)

39P. Mid tibia without an *ad* seta near midlength (Fig. 38). Species of this subgenus are not closely related to the few other siphonines with this state. [Character 24.]

40P. Aristomere 1 very elongate, at least 2X longer than wide (Fig. 15). This state is independently derived in few other, unrelated, siphonines. [Character 9, state L.]

41P. Adults are the smallest of siphonines, with a total length of 2.0-3.0mm. Few other siphonines are typically as small; the average length of adults in other lineages is 3mm or longer. [Character 1.]

42P. Aristomere 3 very short (Fig. 15). [Character 11, state V.]

43S. Crossvein *dm-cu* far removed from wing margin (Fig. 22). This state is also found in few other siphonine lineages, and may not be synapotypic of *S. (Baeomyia)* species. However, the state is obviously homoplastic so is not used here to define a higher subgroup within *Siphona s.l.* [Character 34.]

Siphona (Ceranthia Robineau-Desvoidy)

44P. Adults with cylindrical palpus (Fig. 16). This feature is considered independently derived in two species of *S. (Aphantorhaphopsis)*. [Character 14, state C.]

45P. Pregonite with long seta posteriorly (Fig. 94). The bare state of the pregonite in *S. (Ceranthia)* Mauritius sp. 1 is interpreted as autapotypic. [Character 46, state L.]

46P. Distiphallus with short to long posterolateral arm which is distinctly incised from rest of lateral surface (Fig. 127). The characteristic shape of the distiphallus in *S. (Ceranthia)* species is at least subtlely different from other siphonines which also possess distinct posterolateral projections. [Character 49, states M and E.]

Siphona (Pseudosiphona Townsend)

47P. Pregonite (Fig. 95) broadened in lateral view [character 44, state W], with spinules anterolaterally [character 45, state T] and two to several tiny setae posteriorly [character 46, state F]. Few *S. (Pseudosiphona)* species lack one or another of these states, but other siphonines do not possess more than one.

48P. Distiphallus triangular and anterolaterally spined (Fig. 128). This state is interpreted as that of the groundplan in this subgenus, and the few species which depart from it are regarded as apotypic in this respect.

49S. Labrum of first instars elongate and hook-like in most species (*cf.* Figs. 188-193). Species of *S. (Pseudosiphona)* with a more broadened labrum seem derived from other species in which the labrum is hook-like. Shape of the labrum is a somewhat homoplastic character so this state is ranked as a secondary synapotypy. [Character 64, state N.]

50S. The groundplan condition, and possible synapotypy of this subgenus, is moderately lengthened labella (slightly longer than half prementum length; Fig. 17). [Character 16, state M.]

Siphona (Siphona Meigen)

51P. Proboscis with elongate prementum and labella, with latter at least as long as the former (Figs. 25-26). This state is present in all *S. (Siphona)* species, and convergently present in some other siphonines. [Character 16, state L.]

52S. The male genitalia of *S. (Siphona)* species are remarkably homogeneous for such a large group of species. There is relatively little variation in shapes of pregonite (Fig. 96), surstylus and cerci (Figs. 141, 144), while differences in distiphallus shape (Fig. 129) are more conservative than in any other large siphonine taxon. Perhaps in combination, these features of the male genitalia can be considered synapotypic of the subgenus, though individually none is unique.

Siphona (Siphonopsis Townsend)

53P. Distiphallus tapered to a narrow and truncate tip of varied length (Fig. 130). This state is evidently unique to *S. (Siphonopsis)*.

54S. Labellar length characteristically slightly less than three-fourths prementum length (Figs. 18, 24). This length is not unique to, but is probably synapotypic of, the subgenus. [Character 16, state E.]

Siphona (Uruactia Townsend)

55P. Distiphallus in profile smoothly tapered and apically pointed (Fig. 131). *S. (Aphantorhapha)* species are characterized by a somewhat similar-shaped distiphallus.

There are only two species included in *S. (Uruactia)*, and these are easily recognized as sister species because of several similarities, but each shared state is too widely distributed among other siphonine species to be included here.

6.4 Monophyly of the Proceromyia Mesnil and Entomophaga Lioy lineage

56P. Distiphallus of all four described species characterized by long, spined, anterolateral arm and incised lateral surface (Figs. 108-111). No examined outgroup species or other siphonine has very similar distiphallus features.

57P. Pregonite smoothly curved and apically pointed, with longitudinal ridge which is bare or spined (Figs. 73-76). A spined longitudinal ridge is also present in few New World *Siphona s.l.* species, but the shape of the pregonite is different (Figs. 103-105) and other character states (for example, presence of a seta posteriorly on pregonite as in Figs. 103-104) clearly indicate that these species are not closely related to the *Proceromyia-Entomophaga* lineage. [Character 45, state L.]

6.5 Monophyly of the Peribaea R.-D. and Siphona Meigen lineage

58P. Anal vein extended to wing margin at least as fold (Fig. 22). The groundplan state for the Tachinidae and presumably the Siphonini is anal vein not extended to wing margin. This state in three species of *Actia* is interpreted as independently derived. Andersen (1983) considered *Peribaea* the primitive lineage of the Siphonini and accordingly interpreted anal vein reaching wing margin as synapotypic of the Siphonini and anal vein not reaching wing margin as an apotypic loss in his *Actia* group (*Goniocera, Ceromya* and *Actia*). [Character 33, state E.]

59P. Lower katepisternal seta subequal in length to, or longer than, upper anterior seta (Fig.

32). The near universality of this state within this lineage compared with a shorter lower seta in the outgroup and almost all other siphonines is good evidence that this state is synapotypic of this lineage. Andersen (1983) also polarized a long lower katepisternal seta as apotypic, but interpreted the apotypic state in a more restricted sense. He considered the state in which this seta is longer than the upper anterior seta as synapotypic of Old World *Siphona s.l.* (his *Asiphona*, *Ceranthia* and *Siphona*). This state is the most common among species of world *Siphona s.l.*, but the lower and upper anterior setae are subequal in length in species of some lineages (Table 1). The subequal condition of these setae is found in the majority of *Peribaea* species and is here interpreted as the groundplan state of the *Peribaea-Siphona s.l.* lineage because a short lower seta characterizes all other siphonine lineages. [Character 21, states E and L.]

6.6 Phylogenetics of non-Siphona s.l. siphonine lineages

There are no convincing synapotypies among non-*Siphona s.l.* genera of the Siphonini except those already discussed for the *Proceromyia-Entomophaga* lineage. As equivocal as the generic relationships may be, two characters warrant discussion because the interpretation of their states suggest different phylogenetic scenarios concerning the evolution of *Goniocera*. (No phylogenetic statements about the interrelationships of *Actia*, *Ceromya s.l.* and the *Proceromyia-Entomophaga* lineage are made at this time because no shared states which are phylogenetically interpretable were found among these taxa.)

Goniocera is well established as a monophyletic taxon of the Siphonini (Fig. 210), but its phylogenetic position within the tribe can be interpreted in several ways depending upon the polarization of the states of two characters: (1) length of preapical *ad* seta on fore tibia [character 23], and (2) presence or absence of spinules on the membranous portion of male pregonite [character 45]. The distribution of states for these characters among the four *Goniocera* species and major lineages of the Siphonini is shown in Fig. 211, without polarization of states into plesiotypic and apotypic. The states of three other characters important to the discussion of the phylogenetics of *Goniocera* are also included in Fig. 211.

Length of the preapical *ad* seta on the fore tibia is a difficult character to polarize into plesiotypic and apotypic states. Several species of the outgroup (both species of the Ernestiini, *Triarthria setipennis* and *Neaera robertsonii*; Table 3) have an *ad* seta subequal in length to the preapical *d* seta, but in the others it is short. The character is also varied among siphonines, as documented in Table 1 and Fig. 211, so reversals have presumably taken place in both the outgroup and the Siphonini. Yet the character cannot be dismissed as totally uninformative. The presence of a long preapical *ad* seta in some *Goniocera* species and the four species of *Proceromyia* and *Entomophaga* might represent a synapotypy of these three genera (with a reversal within *Goniocera* and independent acquisitions of the state in two species of *Ceromya s.s.*[7], several *Actia* species and one species of *S. (Aphantorhaphopsis)*). This scenario is illustrated in Fig. 212. The evidence for this interpretation is very weak, though it is worth noting that the members of these three genera are also similar in appearance, with mostly dark coloration and non-vittate, uniformly pruinose abdomens. Are the long preapical *ad* seta and similar appearance of these taxa indicative of their common ancestry, their primitiveness among siphonines, or the result of mosaic evolution and hence of little value in phylogenetic reconstruction? The evolutionary history of *Goniocera* is far from clear because the states of the second character to be discussed are non-congruent with any but the last interpretation.

Considerable weight is here placed upon the presence of spinules on the membranous portion of the male pregonite being an apotypic state [character 45, state M]. This state is considered synapotypic of *Ceromya s.s.* for the reasons discussed in the Phylogenetics section of that taxon. As shown in Fig. 211, this state is also found in *Goniocera io* and apparently nowhere else in the Siphonini. The distribution of this apotypic state can be interpreted in many ways, of which three seem more reasonable than the rest: (1) the state arose independently (and convergently) in *G. io* and *Ceromya s.s.* (Fig. 213), (2) the state arose once, and *Goniocera* and *Ceromya s.s.* are sister groups (with subsequent reversals within both taxa; Fig. 214), or (3) the state arose once, and *Goniocera* is a derived subgroup of *Ceromya*

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[7] the presence of this state in two *Ceromya s.s.* species is discussed in the Phylogenetics section of *Ceromya s.s.*

s.s. (Fig. 215).

Under the first of the above interpretations (illustrated in Figs. 210 and 213), no sister group relationship is indicated between *Goniocera* and another siphonine taxon. Under the next two interpretations (illustrated in Figs. 214 and 215, respectively), the apotypic state is considered synapotypic of *Goniocera* and *Ceromya s.s.* and differ only with respect to the monophyly of *Ceromya s.s.* As discussed elsewhere, the monophyly of *Goniocera* is not in doubt; since the monophyly of *Ceromya s.s.* is based on the character state under discussion, the cladograms in Figs. 214 and 215 are equally parsimonious if the spinulose state of the pregonite is synapotypic of these taxa.

The hypothesis of *Goniocera* and *Ceromya s.s.* sharing a common ancestry at first seems highly improbable, for it requires loss of spinules from the pregonite of all *Goniocera* species except *G. io* as well as loss in many *Ceromya s.s.* species (or non-expression of the apotypic state if it is interpreted as an underlying synapotypy[1]). There is reason to believe that the apotypic state is the groundplan state of *Ceromya s.s.* (as discussed in the Phylogenetics section of that taxon), but not convincingly (or even probably) for *Goniocera*. Instead, the cladograms relating *Goniocera* and *Ceromya s.s.* are presented as alternative (and testable) hypotheses because the distribution of three other male genitalic character states are in congruence with such interpretations. The three characters and their states are shown in Fig. 211 along with the two characters discussed above. If the solid dots for these characters are interpreted as apotypic states, then the shared derived states are present in all examined *Goniocera* species and at least some species of *Ceromya s.s.* and the *C. silacea* species group. Confusing this interpretation is the possibility of these states being primitive, the possibility of homoplasy (note the presence of these states in few other siphonines), and the fact that the three states are not all present in any *Ceromya s.s.* species.

In summary, the phylogenetic position of *Goniocera* among non-*Siphona* siphonines remains enigmatic, with a possible close relationship being indicated between it and the *Proceromyia*-*Entomophaga* lineage (Fig. 212) or *Ceromya s.s.* (Figs. 214-215). Since both these interpretations are highly speculative, the polychotomus (and unresolved) depiction of the origin of *Goniocera* in Fig. 210 is that best reflecting the current state of knowledge of this problem.

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[1] underlying synapotypies are discussed in the next section.

6.7 Phylogenetics of *Siphona* subgenera

Nine subgenera of *Siphona s.l.* are recognized, with all but *S. (Aphantorhaphopsis)* hypothesized as monophyletic (Fig. 210). No clear synapotypies were found at the subgeneric level, though three derived character states which are widely distributed among the subgenera provide some information about possible higher groupings within the genus and weak additional support for its monophyly. These character states, all belonging to characters of the male genitalia, are reviewed below and their phylogenetic significance discussed.

The least informative of the three states concerns shape of the apex of the apical lobe on abdominal sternum 5 [character 39]. As documented in Table 1, the tip of the apical lobe is curved inward in at least some members of most *Siphona* lineages (state C), yet this state is virtually absent from other siphonines (observed in only one *Ceromya s.s.* species). The distribution of state C in the Siphonini suggests that this state is apotypic within *Siphona*, but note that nine of the ten *Siphona* taxa with state C in Table 1 also have state A (apical lobe not curved inward at apex; plesiotypic). This character state distribution may be the result of one or more of the following: (1) homoplasy, possibly resulting from parallel selection (as defined below), (2) reversals to state A from groundplan (and apotypic) state C (also a type of homoplasy, though groundplan state different from that of previous explanation), and/or (3) an underlying synapotypy (as defined below). It is unlikely that the first type of homoplasy alone could account for such a wide distribution of state C among *Siphona* lineages. Equally unlikely is the interpretation of state C as the groundplan state of most *Siphona* lineages with subsequent reversals in almost all lineages. (The groundplan state is clearly A in at least *S. (Siphona)*, as only three unrelated species of the 40-odd species examined for this character possess state C.)

Saether (1979: 305) recognizes two types of parallelisms: (1) "parallelism as a result of *parallel selection* influencing homologous structures" and (2) "parallelism as the result of common inherited genetic factors including parallel mutations, i.e. *underlying synapomorphies*". An underlying synapomorphy (or more generally, synapotypy) has also been described by Saether as "the capacity or tendency to develop parallel similarity" (1977: 31). I suspect that the inwardly curved apical lobe on male sternum 5 results from one of these forms of parallelism, for neither homoplasy nor state reversals provide as satisfactory an explanation for the presence of both states A and C in nine of 13 *Siphona* taxa listed in Table 1. It is not so clear which form of parallelism the shape of the apical lobe is governed by, yet this is the key to its interpretation since, as Saether comments, "parallel selection is of no greater value than convergence, while underlying synapomorphy is comparable to true synapomorphy" (1979: 306). Perhaps there is an inherent tendency (=underlying synapotypy) among most *Siphona* lineages to develop an inwardly curved apical lobe. This would explain both the near ubiquity of state C throughout *Siphona* lineages and its virtual absence from other siphonines. Yet the character in question is also one in which the difference between one state (A) and another (C) involves little change, and the taxa grouped by the presence of the apotypic state seem subjectively no more phylogenetically significant than the polychotomy depicted in Fig. 210. Several factors, including the following, may be involved in expression of state C, all of which contribute to my interpretation of this state as a non-informative apotypic state: (1) state C is not complex so homoplasy may be involved to some degree, (2) there may be a selective advantage to state C which would therefore reduce its phylogenetic value, and (3) *Siphona* lineages from which state C is unrecorded may nevertheless possess the underlying synapotypy.

Two states of the male pregonite are interpreted as apotypic within *Siphona s.l.* because they are absent from all other siphonines. One is presence of spinules on the distal portion of the pregonite [character 45, state T], which is restricted to New World *Siphona* species of subgenera *Actinocrocuta* (Fig. 89) and *Pseudosiphona* (Fig. 95), some members of New World species groups 1 (Fig. 100) and 2, and several unplaced New World *Siphona s.l.*

species (Table 1). The other state, presence of a seta posteriorly on the pregonite [character 46, states T, M, L, F; figures numbers for each state listed in Structural Features chapter], is more widely distributed throughout *Siphona s.l.*, and only unrecorded from subgenera *Siphona* and *Uruactia* (Table 1).

The apotypic states of both pregonite characters are regarded as underlying synapotypies (as defined above) because each involves a novel and complex feature that almost certainly would not arise convergently, nor doubtfully by parallel selection, among so many different lineages. As with the sternum 5 character, some lineages with an apotypic state of the pregonite also have species with a plesiotypic state, so the term underlying synapotypy is preferable to synapotypy, and arguably more correct than postulating a synapotypic groundplan state followed by numerous reversals. The difference in interpretation between the apotypic states of the pregonite and state C of the apical lobe of sternum 5 is primarily due to the greater complexity of the former, though as will become apparent other difficulties in interpretation remain the same. Each pregonite character will be discussed in turn, beginning with the setal character.

A seta posteriorly on the pregonite is a widely distributed, apotypic state among *Siphona s.l.* lineages, though is absent from one or more species of most of these lineages (Table 1). It is particularly evident that lineages in which most species have a tiny seta also have species which lack it, so to some extent there seems to be a graded potential for development of a pregonite seta among *Siphona* lineages (with a large seta almost unique to, and hypothesized as a synapotypy of, *S. (Ceranthia)*). One of the difficulties in interpretation of an underlying synapotypy is how to infer its presence or absence in a taxon from which the apotypic state is unrecorded. Certainly there is no reason to suppose that a pregonite seta is an underlying synapotypy of any non-*Siphona* siphonines, but how does one interpret the absence of the apotypic state in subgenera *Siphona* and *Uruactia*? Only two species of *S. (Uruactia)* are known, and male genitalia of only two specimens were examined, so these findings provide only weak (and inconclusive) evidence for the lack of the underlying synapotypy in this subgenus.

The situation is different for *S. (Siphona)*, as male genitalia of nearly 40 species of this diverse subgenus were examined, and none possess a seta posteriorly on the pregonite. These findings are far from conclusive, but they are suggestive of *S. (Siphona)* occupying a rather primitive position among *Siphona s.l.* lineages. This interpretation is neither supported nor refuted by other characters at this time. It might be argued that a primitive position within *Siphona s.l.* is consistent with the speciose nature and wide geographic distribution of the subgenus, but the conservative features of its many members do not preclude a more recent and rapid radiation of the taxon.

Even if one considers *S. (Siphona)* as a rather primitive lineage of *Siphona s.l.*, it is doubtfully the most primitive. That position probably belongs to certain members of the Old World polyphyletic taxon *S. (Aphantorhaphopsis)*. This subgenus includes species with or without a pregonite seta, and it is possible that some of the latter represent the most primitive lineages of *Siphona s.l.* This interpretation is illustrated in Fig. 216, with *S. (Siphona)* occupying a primitive position relative to most other subgenera, and *S. (Uruactia)* questionably placed near *S. (Siphona)*. Fig. 216 represents one of the more resolved interpretations of the character under discussion, though it must be noted that it is presented as a hypothetical model to be tested, and not as a well corroborated cladogram.

I return now to a consideration of the phylogenetic significance of the field of spinules distally on the sclerotized portion of the pregonite of *S. (Actinocrocuta)* and *S. (Pseudosiphona)* species, some species of New World species groups 1 and 2, and some unplaced New World *Siphona s.l.* species (Table 1 - character 45, state T). Much of the discussion above concerning the pregonite seta applies here as well, as a field of spinules is interpreted as an underlying synapotypy of those taxa in which the state is both present and absent. A cladogram based strictly upon the criterion of presence of the apotypic state in at least one species of a *Siphona* lineage is shown in Fig. 217, but again it must be cautioned that non-expression of this underlying synapotypy in taxa grouped on the left side of the cladogram would lead to misinterpretation of the phylogenetic affinities among these taxa. Of significance is the fact that all taxa grouped by presence of the spinulose state are New World in distribution, and there almost entirely restricted to the tropics and subtropics. Whether or not one or more of the other New World taxa belong in this group, there is at least evidence here for evolution of a higher clade of *Siphona s.l.* within the New World tropics.

One final conclusion can be drawn from the discussion of the three genitalic characters above: the distribution of the apotypic states is consistent with the interpretation of *Siphona s.l.* as a monophyletic lineage, which is independently supported by two synapotypies of first instars (states P32 and P33). Unfortunately the distributions of the apotypic states of these three characters are too phylogenetically equivocal to include as primary or secondary synapotypies of higher clades of *Siphona s.l.*

Figure 210. Cladistic relationships and geographic distribution of the genera and subgenera of the Siphonini. Primary and secondary synapotypies are denoted by the suffixes P and S respectively. The numbered synapotypies are explained in the Evolution chapter and do not correspond to the numbers given to characters in the Structural Features chapter.

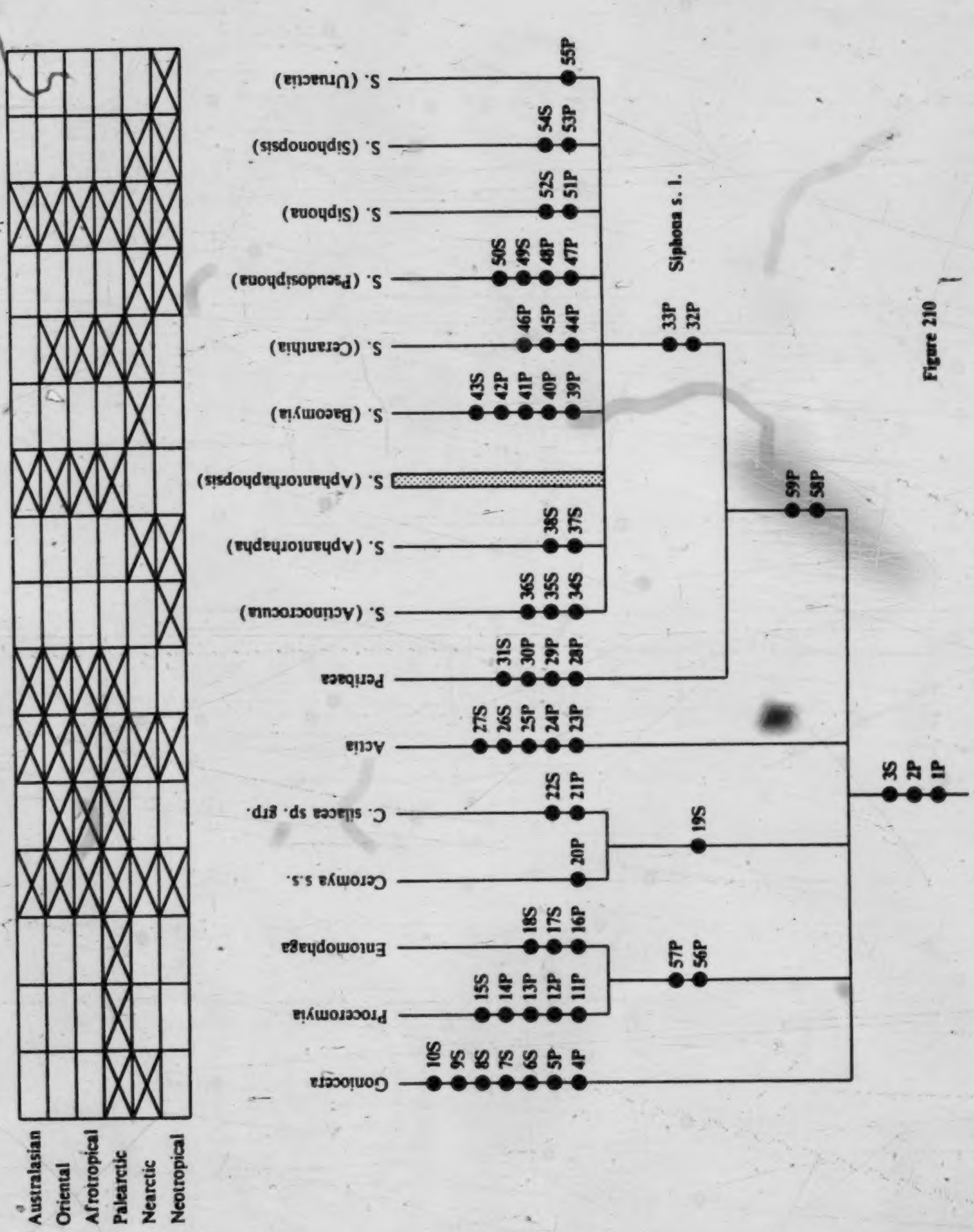

Australasian
Oriental
Afrotropical
Palearctic
Nearctic
Neotropical
Goniocera
Procromyia
Entomophaga
Ceromya s.s.
C. silacea sp. grp.
Actia
Peribaea
S. (Actinocrocuta)
S. (Aphantorhapha)
S. (Aphantorhaphopsis)
S. (Bacomyia)
S. (Ceranthia)
S. (Pseudosiphona)
S. (Siphona)
S. (Siphonopsis)
S. (Uruactia)
Siphona s. l.
10S 9S 8S 7S 6S 5P 4P
15S 14P 13P 12P 11P
18S 17S 16P
57P 56P
20P
22S 21P
19S
27S 26S 25P 24P 23P
31S 30P 29P 28P
36S 35S 34S
38S 37S
43S 42P 41P 40P 39P
46P 45P 44P
33P 32P
50S 49S 48P 47P
52S 51P
54S 53P
55P
59P 58P
3S 2P 1P

Figure 210

Figure 211. Distribution of states for five characters relevant to the interpretation of the cladistic relationships of *Goniocera* B. & B. The male genitalia of *Goniocera montium* were not examined.

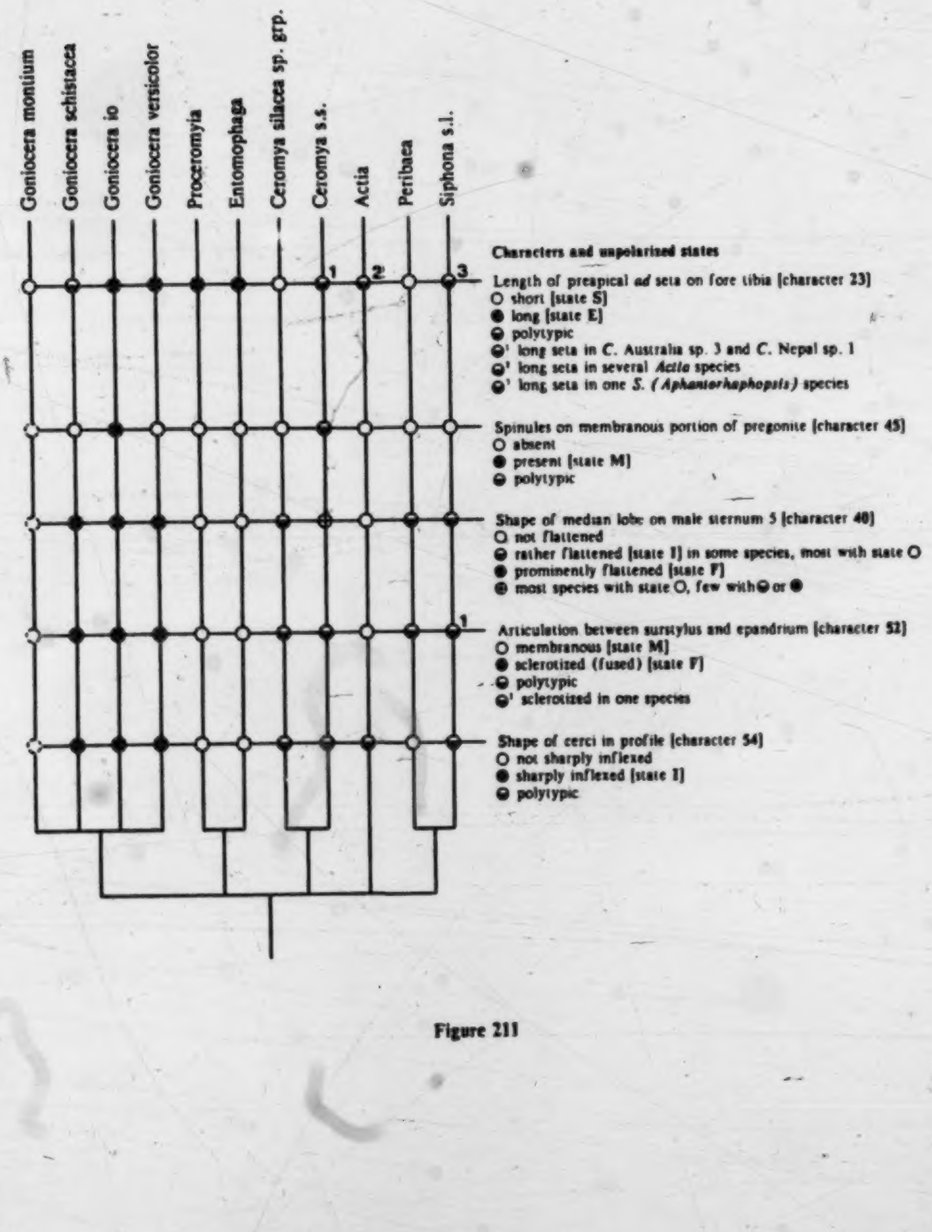

Goniocera montium
Goniocera schistacea
Goniocera io
Goniocera versicolor
Proceromyia
Entomophaga
Ceromya silacea sp. grp.
Ceromya s.s.
Actia
Peribaea
Siphona s.l.
1
2
3
1
Characters and unpolarized states
Length of preapical ad seta on fore tibia [character 23]
○ short [state S]
● long [state E]
◒ polytypic
◒1 long seta in C. Australia sp. 3 and C. Nepal sp. 1
◒2 long seta in several Actia species
◒3 long seta in one S. (Aphantorhaphopsis) species
Spinules on membranous portion of pregonite [character 45]
○ absent
● present [state M]
◒ polytypic
Shape of median lobe on male sternum 5 [character 40]
○ not flattened
◒ rather flattened [state I] in some species, most with state ○
● prominently flattened [state F]
⊕ most species with state ○, few with ◒ or ●
Articulation between surstylus and epandrium [character 52]
○ membranous [state M]
● sclerotized (fused) [state F]
◒ polytypic
◒1 sclerotized in one species
Shape of cerci in profile [character 54]
○ not sharply inflexed
● sharply inflexed [state I]
◒ polytypic

Figure 211

Figures 212 to 215. Varied interpretations of the cladistic relationships of *Goniocera* B. & B. See Fig. 211 for explanation of character states and text for discussion. Open circles indicate plesiotypic states, solid dots indicate apotypic states, and half solid dots indicate the presence of both states within a taxon.

Figure 212. Cladistic relationship of *Goniocera* based on long preapical *ad* on fore tibia as an apotypic state.

Figure 213. Cladistic relationship of *Goniocera* based on independent evolution of spinules on the male pregonite of *Goniocera io* and *Ceromya s.s.* species.

Figure 214. *Goniocera* and *Ceromya s.s.* as sister groups based on spinules on male pregonite as synapotypy.

Figure 215. *Goniocera* as derived subgroup of *Ceromya s.s.*, based on one interpretation of spinules on male pregonite as synapotypy.

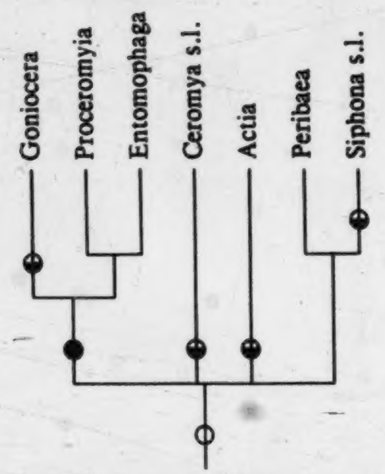

Goniocera
Proceromyia
Entomophaga
Ceromya s.l.
Actia
Peribaea
Siphona s.l.

Fig. 212. Long preapical *ad* seta on fore tibia interpreted as synapotypic of *Goniocera* and the *Proceromyia-Entomophaga* lineage.

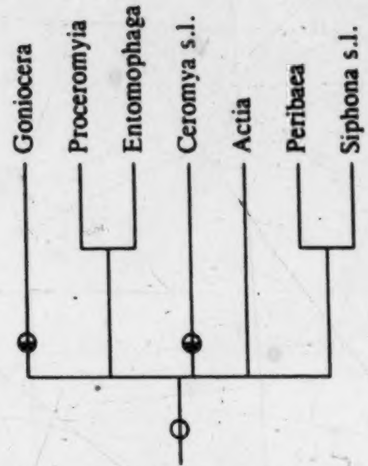

Goniocera
Proceromyia
Entomophaga
Ceromya s.l.
Actia
Peribaea
Siphona s.l.

Fig. 213. Independent evolution of spinules on pregonite of *Goniocera io* and *Ceromya s.s.* (same as Fig. 210).

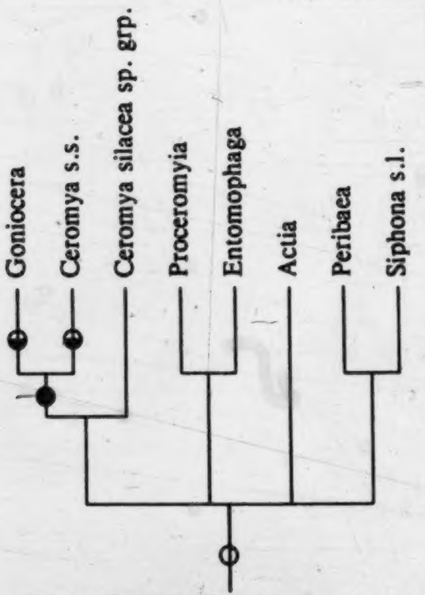

Goniocera
Ceromya s.s.
Ceromya silacea sp. grp.
Proceromyia
Entomophaga
Actia
Peribaea
Siphona s.l.

Fig. 214. Spinules on pregonite interpreted as synapotypic of *Goniocera* and *Ceromya s.s.*

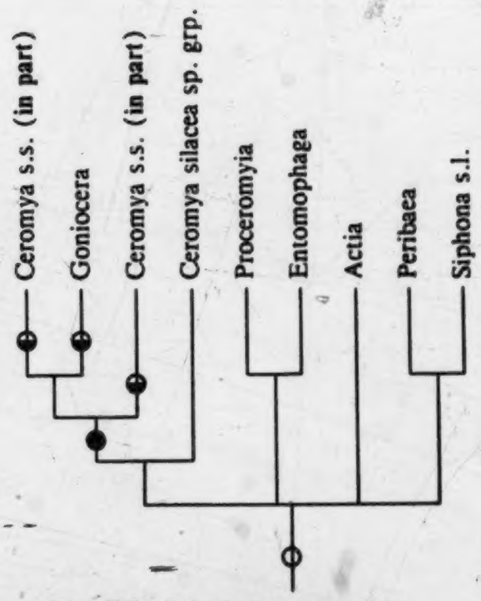

Ceromya s.s. (in part)
Goniocera
Ceromya s.s. (in part)
Ceromya silacea sp. grp.
Proceromyia
Entomophaga
Actia
Peribaea
Siphona s.l.

Fig. 215. Spinules on pregonite interpreted as synapotypic of *Goniocera* and *Ceromya s.s.*, with the former a derived subgroup of the latter.

Figures 212-215. Varied interpretations of the cladistic relationships of *Goniocera* B. & B.

Figure 216. One interpretation of the cladistic relationships within *Siphona s.l.*, based on presence of a seta posteriorly on male pregonite as synapotypy.

Figure 217. One interpretation of the cladistic relationships within *Siphona s.l.*, based on presence of spinules on the sclerotized portion of male pregonite as synapotypy.

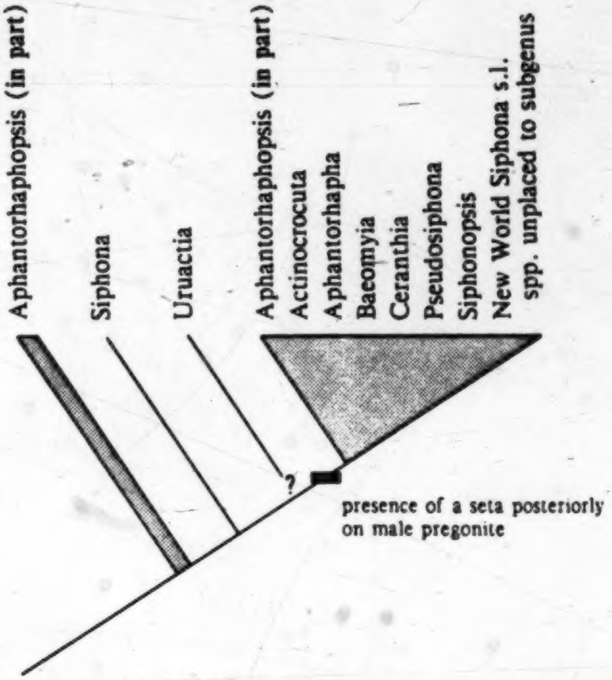

Aphantorhaphopsis (in part)
Siphona
Uruactia
Aphantorhaphopsis (in part)
Actinocrocuta
Aphantorhapha
Baeomyia
Ceranthia
Pseudosiphona
Siphonopsis
New World Siphona s.l.
spp. unplaced to subgenus
?
presence of a seta posteriorly
on male pregonite

Figure 216

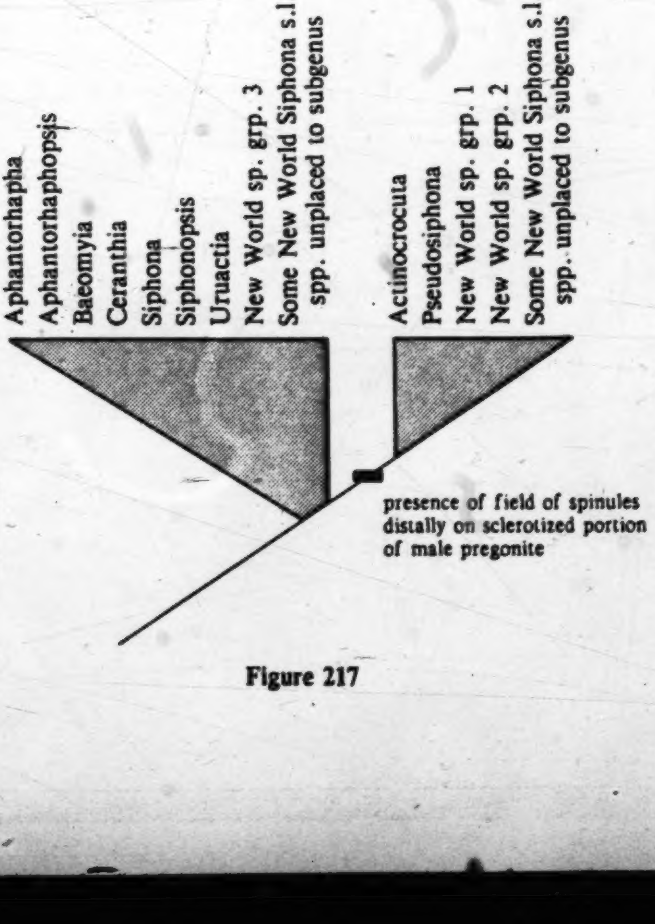

Aphantorhapha
Aphantorhaphopsis
Baeomyia
Ceranthia
Siphona
Siphonopsis
Uruactia
New World sp. grp. 3
Some New World Siphona s.l.
spp. unplaced to subgenus
Actinocrocuta
Pseudosiphona
New World sp. grp. 1
New World sp. grp. 2
Some New World Siphona s.l.
spp. unplaced to subgenus
presence of field of spinules
distally on sclerotized portion
of male pregonite

Figure 217

6.8 Evolutionary trends

I discussed in an earlier paper (O'Hara 1983a) the trend toward a long proboscis in *S. (Siphona)* species - a trend also evident in one or more *Actia* species groups and several other lineages of *Siphona s.l.* (character 16, Table 2). Three other trends among siphonines became apparent during this revision of the tribe. Two involve characteristics of the female genitalia:

1) trend toward an extensible ovipositor, involving elongation of genitalic sclerites and/or intersegmental membrane (character 55, Table 2; most pronounced in some *Peribaea* species - Figs. 155-156).

2) trend toward a ventrally keeled ovipositor, involving posteromedial surface of segment 7 (character 59) and also, in few species, the posteromedial surface of segment 6 (character 56).

Both these trends probably reflect adaptations of larvipositing females to their hosts, but too little is known about host searching and larviposition in siphonines to correlate these behaviors with the above trends. Perhaps, as suggested by Andersen (1983: 8), more specialized ovipositors belong to siphonines that larviposit directly on their hosts.

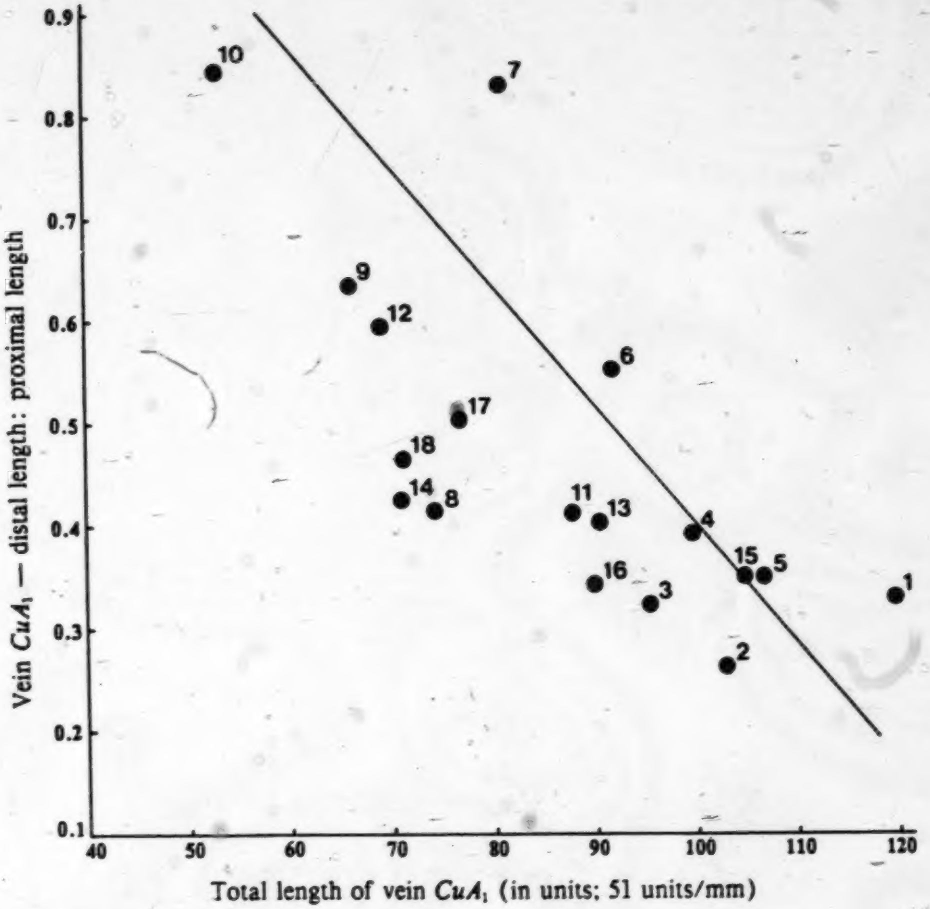
The only evolutionary trend amenable to direct analysis is position of wing crossvein *dm-cu* (character 34). Primitively (as judged by outgroup and ingroup comparisons), this crossvein meets vein CuA_1 in the distal sector of that vein (Fig. 21). The more derived condition is for *dm-cu* to be further removed from the wing margin (Fig. 22).

A measure of *dm-cu* position was obtained by dividing the distal length of CuA_1 by its proximal length (as explained in the Structural Features chapter, character 34). Accordingly, taxa with the primitive *dm-cu* condition have low values for this ratio and more derived taxa have high values (Table 2). Considerable variation in position of *dm-cu* exists within most siphonine lineages, though the generally low standard deviation for each lineage indicates that most lineages have a relatively characteristic *dm-cu* position. It is evident from these data that moderately derived crossvein states characterize *Actia*, *S. (Aphantorhapha)* and *S. (Pseudosiphona)*, and highly derived states characterize *Peribaea* and *S. (Baeomyia)*.

If one were to consider position of crossvein *dm-cu* in siphonines as an evolutionary transformation series, with the highest value for the ratio above representing the most derived state, then the cladistic grouping of siphonine taxa would be incongruent with that illustrated in Fig. 210. Further analysis of crossvein data indicates that this interpretation is invalid, because position of crossvein *dm-cu* is correlated with wing size (and hence, indirectly, with body size).

Plotted in Fig. 218 are the means for total length of CuA_1 (on *X*-axis) and ratio of distal length: proximal length of vein CuA_1 (on *Y*-axis) for 18 lineages of the Siphonini (excluding polyphyletic groups *S. (Aphantorhaphopsis)* and New World unplaced *Siphona s.l.* species). The linear regression line is shown, as calculated from the means of the 18 taxa. The correlation coefficient of -0.70 is statistically significant, indicating that a correlation exists between position of crossvein *dm-cu* and length of CuA_1 - by extrapolation, *dm-cu* tends to be further from the wing margin in smaller siphonines than in larger ones. (This trend is not a function of allometry, as small specimens of a species have similar *dm-cu* position to larger specimens.) It is inferred from these data that small siphonines (particularly in the range of 2-3mm in length) benefit from having *dm-cu* positioned relatively far from the wing margin. Possibly, the increased flexibility in the posterior part of the wing is aerodynamically advantageous to small siphonines.

Figure 218. Correlation between position of wing crossvein *dm-cu* and length of wing vein *CuA_1*. Values are plotted for 18 taxa of the Siphonini. The linear regression line is shown (*Y* intercept of 1.11, slope of -0.007 and correlation coefficient of 0.70).



Numbers refer to the following taxa:

1 — *Goniocera*
2 — *Proceromyia*
3 — *Entomophaga*
4 — *Ceromya s.s.*
5 — *Ceromya silacea* sp. grp.
6 — *Actia*
7 — *Peribaea*
8 — *S. (Actinocrocuta)*
9 — *S. (Aphantorhapha)*
10 — *S. (Baeomyia)*
11 — *S. (Ceranthia)*
12 — *S. (Pseudosiphona)*
13 — *S. (Siphona)*
14 — *S. (Siphonopsis)*
15 — *S. (Uruactia)*
16 — New World *Siphona* sp. grp. 1
17 — New World *Siphona* sp. grp. 2
18 — New World *Siphona* sp. grp. 3

Figure 218

6.9 Historical zoogeography

The Siphonini are not ideal for zoogeographic analysis, because they are unknown from fossils, their sister group has not been determined and their phylogenetic history is not well resolved. It is therefore necessary to take a general approach to interpreting their zoogeographic history. Accordingly, I draw very heavily upon the studies of others concerning both physical and biotic aspects of earth history to help infer a little about how siphonines came to be distributed as they are. Emphasis is placed in this section on interpreting the geographic history of New World siphonines.

The geographic distribution of the major lineages of the Siphonini are ~~detailed in~~ the species lists and Geographic Distribution sections of the Classification chapter, and summarized by region in Fig. 210. Eight patterns of distribution are evident among these lineages:

(1) cosmopolitan — *Ceromya s.s.*, *Actia* and *S. (Siphona).*

(2) widespread Old World-Nearctic — *S. (Ceranthia).*

(3) widespread Old World — *Ceromya silacea* species group, *Peribaea* and *S. (Aphantorhaphopsis)* (the latter is polyphyletic or paraphyletic with respect to other *Siphona s.l.* species, but is apparently without close affinities with New World *Siphona s.l.* species).

(4) Holarctic — *Goniocera.*

(5) Palearctic — *Proceromyia* and *Entomophaga.*

(6) Nearctic — *S. (Baeomyia).*

(7) Nearctic-Neotropical — *S. (Aphantorhapha)*, *S. (Pseudosiphona)*, *S. (Siphonopsis)* and New World *Siphona* species groups 2 and 3.

(8) Neotropical — *S. (Actinocrocuta)*, *S. (Uruactia)* and New World *Siphona* species group 1.

Absent from the above patterns is any taxon of widely, and strictly, Southern Hemisphere distribution. Similarly, no such pattern is evident among species groups of the three cosmopolitan taxa. This negative evidence suggests that the Siphonini did not diversify in the Southern Hemisphere until after the breakup of Gondwanaland, either because they were initially of Laurasian distribution or they evolved somewhere in the Southern Hemisphere after South America, Africa and Australia drifted apart.

Breakup of Gondwanaland began with the separation and northward movements of Africa and India from the other southern continents, followed by separation of South America and then Australia from Antarctica. Timing of each of these events is inexactly known, though most workers agree that South America and Africa were in close proximity until the Late Cretaceous, and South America and Australia were narrowly jointed *via* Antarctica (or only narrowly separated) into the Early Tertiary (Adams 1981, Smith *et al.* 1981). Not only is the geologic timing of these events important to the zoogeographer, but also the varied dispersal abilities of different organisms and the changing environmental conditions of the Cenozoic. All of these factors affected the probability of particular organisms reaching new habitations.

Siphonines are moderately good dispersers, as judged from their limited species numbers on Madagascar and islands of the Caribbean and southeast Asia, and their virtual absence from mid-oceanic islands. This ability to cross moderate water gaps implies that siphonines cross barriers more readily than most terrestrial vertebrates, and can doubtfully cross such large distances as those now between South America, Africa and Australia.

I infer from the lack of a Gondwanaland distribution pattern among siphonines, the timing of the breakup of Gondwanaland and the dispersal powers of siphonines, that the history of the Siphonini in the Southern Hemisphere is entirely Cenozoic in age. This age could be extended to the Late Cretaceous if southern continents were farther apart at the beginning of the Cenozoic (or siphonines poorer dispersers) than here suggested.

I noted above that siphonines might have originated in Laurasia prior to the breakup of Gondwanaland (*i.e.* during the Cretaceous). This possibility cannot be corroborated or rejected by an analysis of siphonine relationships and present day distributions (Fig. 210). Instead, such an early age for the Siphonini is considered highly unlikely because fossil Calyptratae are virtually unknown from pre-Tertiary deposits, and extant calyptrates show few and suspect Gondwanian distributions (O'Hara 1983a: 329).

In summary, no evidence supports a pre-Tertiary origin of the Siphonini. Therefore, in the ensuing discussion, all aspects of the zoogeographic history of the Siphonini are couched in terms of Cenozoic events.

Large and small scale Cenozoic changes in earth climate, sea level, biotic associations and position and topography of continents must have produced a shifting array of physical and ecological barriers to the dispersal of siphonines. The interpretation of siphonine distribution patterns is inferred from a comparison of siphonine distribution (and hypothesized relationships) with major changes in earth history. As an introduction to the analyses of siphonine distributions, some of the major physical and ecological changes that are thought to have occurred during the Cenozoic are outlined. Most of this account is summarized from Adams (1981), with additions as noted.

Europe and Asia became separated by the Turgai Strait during Early Tertiary time, while the Tethys Sea slowly narrowed as Africa and India drifted northward. South America, severed from Africa in the Cretaceous and from Antarctica in the Late Paleogene, remained isolated from other land masses until the Pliocene. North America was in land contact with both Europe and Asia in the Early Tertiary. Two or three land bridges spanned the North Atlantic during the Paleogene, providing good avenues for biotic exchange between North America and Europe during most of this period. Though the histories of these land bridges are geologically complex and difficult to interpret, remnants of a North Atlantic corridor might have persisted even into the Miocene (Matthews 1979, Eldholm and Thiede 1980, McKenna 1983). However, scanty fossil evidence of a functional Miocene corridor implies that it was, at best, a weak filter bridge at that time (also, Beringian interchange at that time could have produced similar fossil distributions).

Beringia probably provided a land corridor between Asia and North America throughout most of the Cenozoic until periodically submerged during the Quaternary (McKenna 1983). However, Beringia occupied a more northerly position with respect to the earth's rotational pole during the Early Tertiary, so probably experienced a more extreme climate at that time than its North Atlantic counterpart. Hence, Beringia might have functioned more as a filter bridge than a land bridge in the Early Tertiary before assuming a relatively more southern postion (McKenna 1983).

The climate during the Paleogene was considerably warmer than now even at high latitudes, peaking during the Early Eocene after several warm-cool fluctuations (Wolfe 1978, 1980, Axelrod 1983, Romero 1986). By Middle Eocene the earth's climate had begun to deteriorate, causing retreat of paratropical forests (*sensu* Wolfe 1978) from high latitudes and their replacement with more temperate adapted elements. By the end of the Paleogene a seaway opened between Antarctica and Australia, and the Turgai Straits closed between Europe and Asia.

Climatic cooling continued, with periodic fluctuations, in the Neogene. Faunal exchange increased between Africa and Eurasia as the Tethys Sea narrowed, though changes in sea level alternately facilitated and hindered such exchange, as it did also as the Australian plate converged upon the island archipelago of southeast Asia (Martin 1982). Large scale climatic and biotic changes took place as the Tethys Sea closed and major mountain building occurred, particularly between Asia and the Indian subcontinent and along the western edge of the Americas. Antarctica grew progressively colder, with development of a polar ice cap in the Late Miocene (Mercer and Sutter 1982). Marked increase in exchange between North and South America began in the Pliocene with the emergence of a land corridor between these continents, which has persisted under changing ecological regimes to the present day. Most dramatic of all were the wide scale changes to the earth's climate and biota during the ice ages of the Pleistocene.

The following discussion about the zoogeographic history of the Siphonini is partly based on three important assumptions: (1) siphonine evolution and diversification took place under the general Cenozoic conditions just described, (2) siphonines were more likely to shift geographically than ecologically in the face of changing climatic conditions (in the same way as most species are thought to have responded to Pleistocene climatic changes, for example), and (3) general patterns of siphonine distribution have not been profoundly limited by host availability (one might expect that siphonines, as parasitoids, have been constrained in their ability to diversify in newly invaded regions by lack of suitable hosts, yet no such constraints appear to have affected siphonine distributions).

Two patterns of distribution are recognized among strictly Old World siphonines - one Palearctic and the other widespread (see list of patterns at beginning of section). The Palearctic pattern is shared by sister genera *Proceromyia* (with two eastern species) and *Entomophaga* (with two western species). A past vicariance of a widespread ancestor into an eastern *Proceromyia* and western *Entomophaga* lineage is the most obvious explanation for this pattern. However, these lineages may be relatively basal to siphonine phylogeny, so might once have been more diverse (and possibly more widespread) than at present. This might also account for the marked external differences among the extant species. On the other hand, the restriction of extant species to the Palearctic region, and a temperate environment, is suggestive of a more recent origin (perhaps during the Miocene when temperate forests reached their maximum extent; Graham 1972, Axelrod 1983).

Belonging to the second Old World distribution pattern are *Peribaea*, the *Ceromya silacea* species group and *S. (Aphantorhaphopsis)*. *Peribaea* is widespread throughout all Old World regions, with more described species in the Australian region than any other siphonine lineage (partly, but not entirely, a reflection of recent taxonomic work by Shima 1970a). *Peribaea* species are also recorded from such islands as Fiji, Seychelles, Mauritius and Madagascar, so it is paradoxical that this highly vagile and speciose group has not reached the New World.

Little can be written about the distributions of the *Ceromya silacea* species group and *S. (Aphantorhaphopsis)* except that they, like other widespread taxa except *Peribaea*, have depauperate faunas in the Australian region. This pattern undoubtedly reflects the isolation of Australia, New Guinea and associated islands from Asia during most of the Cenozoic.

Two distribution patterns, those of *Goniocera* and *S. (Ceranthia)*, have Nearctic-Old World elements. The former is known from four temperate species, one in eastern North America and three in Europe. The phylogenetic relationships among these species are unknown, though the presence of possible sister groups to *Goniocera* in the Old World suggests that the genus arose there. Later dispersal to, and differentiation in, the New World probably occurred when temperate forests were widespread at high latitudes and continuous between North America and Eurasia. Such conditions developed during the Early Neogene, presumably after severance of a functional North Atlantic land bridge (though Axelrod (1983) hypothesizes exchange of temperate forest elements across both Beringia and a North Atlantic corridor in the Miocene). Therefore, barring long range dispersal from Europe, entry to the New World was probably through Beringia. The restricted ranges of the extant species, all far removed from Beringia yet cool adapted, are best accounted for by either an Early Neogene vicariance of a Holarctic species (with changes in range due to Miocene mountain building and global climatic changes), or a more recent vicariance followed by Pleistocene displacements (Fig. 219).

The subgenus *S. (Ceranthia)* also has a Nearctic-Old World distribution pattern. Old World species of this subgenus are almost equally split in number between the Palearctic and Afrotropical regions, while the Nearctic element is strictly temperate. As with *Goniocera*, the temperate element of *S. (Ceranthia)* in the Nearctic region probably resulted from dispersal from the Old World during the Neogene (Fig. 219), possibly during the Miocene judging from the moderate number of Nearctic species (mostly undescribed).

Among the remaining distribution patterns are four *Siphona* lineages only recorded from either the Nearctic (*S. (Baeomyia)*) or Neotropical (*S. (Actinocrocuta)*, *S. (Uruactia)* and New World *Siphona* species group 1) region. In patterns such as these where all members of a lineage are within one region, it is most parsimonious to postulate that each lineage evolved from an ancestral species in that region. This is almost certainly true of the three Neotropical lineages, since *S. (Uruactia)* is only known from two species in Peru and Ecuador, and *S. (Actinocrocuta)* and N.W. *Siphona* sp. grp. 1 are members of a monophyletic group (Fig. 217) of almost entirely Neotropical distribution. The history of Neotropical siphonines is discussed in more detail further on.

Three siphonine lineages have cosmopolitan distributions: *Ceromya s.s.*, *Actia* and *S. (Siphona)*. The zoogeographic history of *S. (Siphona)*, with special emphasis on the North American fauna, was treated elsewhere (O'Hara 1983a). I hypothesized that periodic exchange between the Old and New World took place among *S. (Siphona)* species groups from the Eocene to the Pleistocene. In general, Holarctic elements were hypothesized as Middle Tertiary to Quaternary in age (Fig. 219) and more tropically distributed taxa with Old World-New World affinities of older ancestry (Fig. 220). I predict that similar hypotheses can explain the distributions of *Ceromya s.s.* and *Actia* species groups when these are phylogenetically analyzed.

It would appear from lists of described species that cosmopolitan lineages of the Siphonini are low in species diversity in both the Neotropical and Australian regions. Though this is so for the Australian region, it is not for the Neotropical region. The pattern of low diversity in the Australian region is the same as for most Old World siphonine lineages with Australian members, reflecting the relative isolation of that region from Asia for most of the Cenozoic (see above). South America was also isolated from other continents for most of the Cenozoic, so the high diversity of siphonines in that region poses an especially interesting zoogeographic problem.

The Neotropical region has three endemic siphonine taxa (*S. (Actinocrocuta)*, *S. (Uruactia)* and New World *Siphona* species group 1), five lineages shared only with the Nearctic region (*S. (Aphantorhapha)*, *S. (Pseudosiphona)*, *S. (Siphonopsis)* and New World *Siphona* species groups 2 and 3), and elements of three cosmopolitan groups (*Ceromya s.s.*, *Actia* and *S. (Siphona)*). How can this high diversity of Neotropical siphonines be explained? Whether the ancestors of most Neotropical lineages originated in that region or in the Old World is of minor importance, as the major pathways of movement (*i.e.* between the Americas and between North America and Eurasia) would be the same even if the direction were reversed. The phylogenetic relationships are presently too inadequately known in *Ceromya s.s.*, *Actia* or *S. (Siphona)* to strongly argue for or against an Old World origin of each (*cf.* O'Hara 1983a, in which an Old World origin was favored partly because the high diversity of these taxa in the Neotropical region was unknown). However, the possibly basal lineages of the Siphonini are Old World in distribution, so for the purpose of this discussion an Old World origin will be assumed for these three taxa. Certain lineages of *Siphona s.l.* are certainly New World in origin, as the distributions in Fig. 210 and possible relationships in Fig. 217 illustrate.

It follows from the review above about Cenozoic events and general assumptions about siphonine evolution, that the only route to (or from) South America during the Cenozoic would have been through North America. It is well known on the basis of both geologic and fossil evidence that South America was physically isolated from other continents during most of the Cenozoic. However, there were two periods of faunal and floral exchange with North America. The first is hypothesized as Paleocene (and Late Cretaceous), as evidenced and/or postulated from geologic evidence (Coney 1982) and distributions of angiosperms (Gentry 1982), herpetofauna (Savage 1982, Estes and Báez 1985), atherinid fishes (White 1985), colubrid snakes (Cadle 1985) and mammals (Gingerich 1985, Webb 1985a). The exact nature of the Paleocene connection is uncertain, though there is general agreement that it was probably an island chain and functioned as a filter bridge. Certain organisms evidently crossed this bridge more readily than others. The suggestion that this filter bridge persisted into the Eocene is not well documented.

The second period of biotic exchange between the Americas is very well corroborated and the subject of a recent multi-authored book, "The great American biotic interchange" (Stehli and Webb 1985). This interchange began in the Pliocene (about 3mybp [million years before present] according to most sources, but 5mybp according to others) with the emergence of a complete land corridor between the Americas. This corridor has alternately functioned, from that time to the present, as a route of dispersal for certain organisms and a barrier to others, as global climate fluctuated throughout the ice ages of the Pleistocene.

It is extremely doubtful that the diversity of Neotropical Siphonini can be entirely accounted for by immigrations since the Pliocene, though it is clear that present day siphonine sister species and sister groups distributed between Middle and South America are evidence of siphonine participation in the "great biotic interchange". The important question to be addressed here is whether earlier siphonine arrivals to South America were over a water gap or across a filter or land bridge.

Assuming (as above) that siphonines originated in the Old World during the Cenozoic and have generally maintained their ecological affinities during periods of major climatic change, it follows that ancestors of extant Neotropical siphonines entered North America from Eurasia at a time during the Tertiary when land bridges between the continents were subtropical to tropical in nature. As the only such land bridges were at high latitudes (Beringia and across the North Atlantic), and the climatic optimum of the Early Eocene was the only time during the Tertiary that these corridors supported such conditions, it is hypothesized that an ancestral stock of Neotropical Siphonini entered the New World at that time. (Webb, comparing mammal faunas of Europe and North America, called the warm period of the Early Eocene "the most intensive intercontinental interchange between any two continental mammal faunas before the Great American Interchange." (1985a: 207)) Then, as global climate cooled in the latter part of the Paleogene and temperate forests began to replace the retreating tropical forests, siphonines became increasingly more southerly distributed in North America (Fig. 220). This sequence of events was proposed to explain Mexican elements of *S. (Siphona)* (O'Hara 1983a), and to explain some elements of the Central American herpetofauna (Savage 1982).

The zoogeographic scenario has thus far tended toward a vicariant explanation of siphonine history. However, only dispersal events over a wide water gap or across a weak filter bridge can account for the earliest siphonine entries into South America (Fig. 220). Even if siphonines colonized North America in the Eocene and reached the southern part of the continent shortly thereafter, they would still have arrived too late to cross the Paleocene filter bridge into South America. There is no evidence from the Eocene to the Miocene of a land corridor between the Americas, and little evidence for an even weak filter bridge until the Late Miocene. (An intermittent filter bridge is mostly hypothesized to explain the first appearance of certain organisms in the fossil record of either North or South America - *e.g.*

Stehli and Webb 1985, Chapter 1.) Whether or not a filter bridge existed from time to time during this interval, there is nevertheless a suggestion of faunal and floral exchange, as inferred from cricetine rodents (Hershkovitz 1966, 1972), angiosperms (Raven and Axelrod 1975), carabid beetles (Ball 1978, Allen and Ball 1980, Ball and Shpeley 1983, Noonan 1985), mammals (Webb 1985b), ectoparasites of mammals (Wenzel and Tipton 1966), primates and caviomorph rodents (Wood 1985 [though the zoogeographic interpretations of these groups are highly controversial]) and herpetofauna (Vanzolini and Heyer 1985). Siphonines, like these taxa, seem to have preceded, as well as participated in, the "great biotic interchange" in their colonization of South America. When, and how often, is uncertain. The large clade of Neotropical *Siphona s.l.* species (Fig. 217) suggests at least a moderate history in South America (Oligocene or Miocene?). The high species diversity of *Ceromya s.s.*, *Actia* and *S. (Siphona)* in the Neotropics also suggests that members of these lineages reached South America before formation of the Pliocene land bridge (Fig. 220).

A minor element of the Nearctic siphonine fauna is possibly derived from tropical adapted siphonines. Two sources are hypothesized: Firstly, differentiation of temperate adapted taxa from tropical adapted taxa as subtropical to tropical conditions over most of the region were replaced by warm temperate to boreal conditions after the climatic deterioration of the Eocene. (Similar to the hypothesis that the vegetation of the Sonoran Desert is mostly derived from contiguous, less arid adapted, taxa; Axelrod 1979.) It has been assumed throughout this section that the evolution of new ecological affinities such as this have played a minor role in the history of New World Siphonini - an analysis of relationships among North American *S. (Siphona)* suggests this is a valid assumption (O'Hara 1983a). Secondly, few Nearctic taxa are likely derived from reinvasion of the region from Middle or South America (Fig. 219). Most of these taxa are southerly distributed in the Nearctic region.

Perhaps as more organisms are studied, particularly vagile organisms like many insects, vicariance biogeographers will recognize biotic exchange between North and South America as a zoogeographic problem demanding of both dispersal and vicariant explanations. Cracraft (1975), for instance, considered the patterns of distribution between the Americas as inadequately interpretable by vicariant events alone. It must be realized that in certain areas dispersal cannot be ignored in favor of the "rigorous" method of vicariance biogeography. Erwin, discussing how vicariance biogeographers interpret distributional data, wrote:

> The major flaw of the entire Croizat school [vicariance biogeography] is that their method is no more "general" [meaning "vicariance ... is to be assumed and dispersal only explains special cases"] than that of the dispersal or centrist's school, because biological organisms are not generalists! All groups and subsets of groups have their own unique powers of movement or lack of movement and each group must be dealt with on its own merits with full knowledge of powers of dispersal, passive or active, or lack thereof." (1979: 357)

Summary of the zoogeographic history of the Siphonini

(1) The Siphonini are hypothesized as originating during the Cenozoic, because of the virtual absence of Mesozoic fossil Calyptratae and lack of recognizable Gondwanian distributions among extant siphonines.

(2) The present distributions of sister genera *Proceromyia* and *Entomophaga* in eastern and western Palearctic, respectively, suggest a past vicariance of a widespread Palearctic ancestor. However, the possibly rather basal position of this clade in the Siphonini might reflect an older ancestry than otherwise suspected.

(3) A general pattern of low diversity is noted in the Australian region for most siphonine lineages. This pattern is explained by the relative isolation of Australia and associated islands from southeast Asia during most of the Tertiary.

(4) It is assumed from largely inferential evidence that the Siphonini originated in the Old World, so the high diversity of New World siphonines must be explained by northern routes of entry (across Beringia and the North Atlantic) from Eurasia (Figs. 219, 220).

(5) Most Nearctic siphonines are descendants of Old World taxa that became widespread in the Holarctic region since the Middle Tertiary, as temperate and boreal conditions replaced the more tropical conditions of the Eocene (Fig. 219). A minor component of the Nearctic fauna is derived from tropical adapted siphonines. These either differentiated *in situ* from tropical adapted siphonines as global climate cooled and temperate forests expanded, or reinvaded the Nearctic region from Middle or South America (Fig. 219).

(6) It is assumed that siphonines have generally maintained their ecological affinities through periods of climatic change. Therefore, Neotropical siphonines are hypothesized as descendants of Old World, tropical adapted, siphonines that became widespread in the Holarctic region during the climatic optimum of the Eocene. Subsequent deterioration in climate and periodic crossing of a water barrier (weak filter bridge?) between the Americas during the Middle to Late Tertiary, and speciation in South America, accounts for the high diversity of some siphonine lineages in the Neotropical region (particularly the large clade of Neotropical *Siphona s.l.* species) (Fig. 220).

(7) Sister species and groups distributed on either side of the Isthmus of Panama (mostly Middle America-South America) are evidence of siphonine participation in the "great American interchange" of the Pliocene and Quaternary.

Predictions and tests of zoogeographic hypotheses

(1) No Gondwanian distribution patterns will be recognized among siphonines.

(2) More resolved phylogenies of both higher taxa and species groups of the Siphonini will more firmly establish the Old World origin of most lineages and corroborate the suspected affinities between Nearctic and Palearctic Siphonini (*i.e.* similar relationships are expected to those hypothesized for *S. (Siphona)*; O'Hara 1983a).

(3) The largely endemic nature of Neotropical Siphonini will become apparent as relationships to faunas of other regions are resolved, reflecting the old origin of the fauna from Early Eocene, North American, ancestors.

(4) Indirect corroboration will be forthcoming from similar interpretations of Neotropical elements of similarly distributed taxa, and corroboration or refutation of aspects of earth history herein reviewed.

Figure 219. General zoogeographic history of Nearctic elements of the Siphonini. Three ancestral sources are hypothesized as contributing to the siphonine fauna of the Nearctic region:

(1) most taxa are derived from Old World ancestors crossing Beringia from the Middle Tertiary to the Pleistocene. These taxa evolved in association with warm temperate to boreal biomes.

(2) a minor component is derived from *in situ* differentiation, as tropical adapted siphonines shifted southward, and temperate forests expanded, following the climatic deterioration of the Eocene.

(3) another minor component, mostly southern Nearctic in distribution, are taxa that reached the Nearctic region from Middle or South America. Taxa reaching North America from South America did so either before (very few taxa) or after a land corridor was established between these continents in the Pliocene.

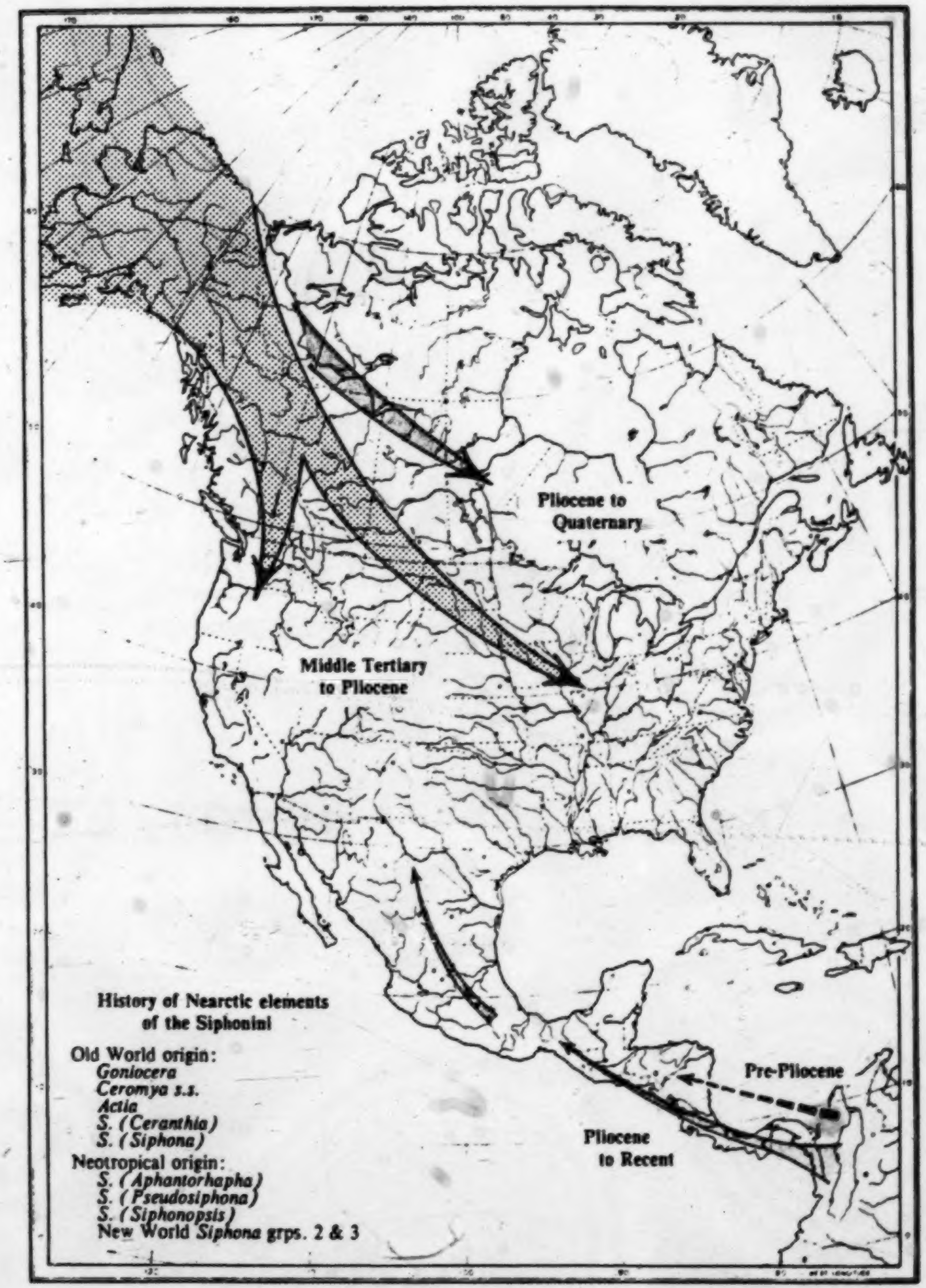

Pliocene to
Quaternary
Middle Tertiary
to Pliocene
Pre-Pliocene
Pliocene
to Recent
History of Nearctic elements
of the Siphonini
Old World origin:
Goniocera
Ceromya s.s.
Actia
S. (Ceranthia)
S. (Siphona)
Neotropical origin:
S. (Aphantorhapha)
S. (Pseudosiphona)
S. (Siphonopsis)
New World *Siphona* grps. 2 & 3

Figure 219

Figure 220. Pre-Pliocene zoogeographic history of Neotropical Siphonini. An ancestral stock of tropical adapted siphonines are hypothesized to have reached North America across Beringia and/or North Atlantic land bridges during the climatic optimum of the Early Eocene. These taxa became more southerly distributed as global climate deteriorated. In the absence of a land bridge between the Americas for most of the Cenozoic, ancestral siphonines of several major lineages crossed a water gap (weak filter bridge?) to reach South America. Exchange was facilitated between the Americas after establishment of a land corridor in the Pliocene (as siphonines participated in the "great American interchange").

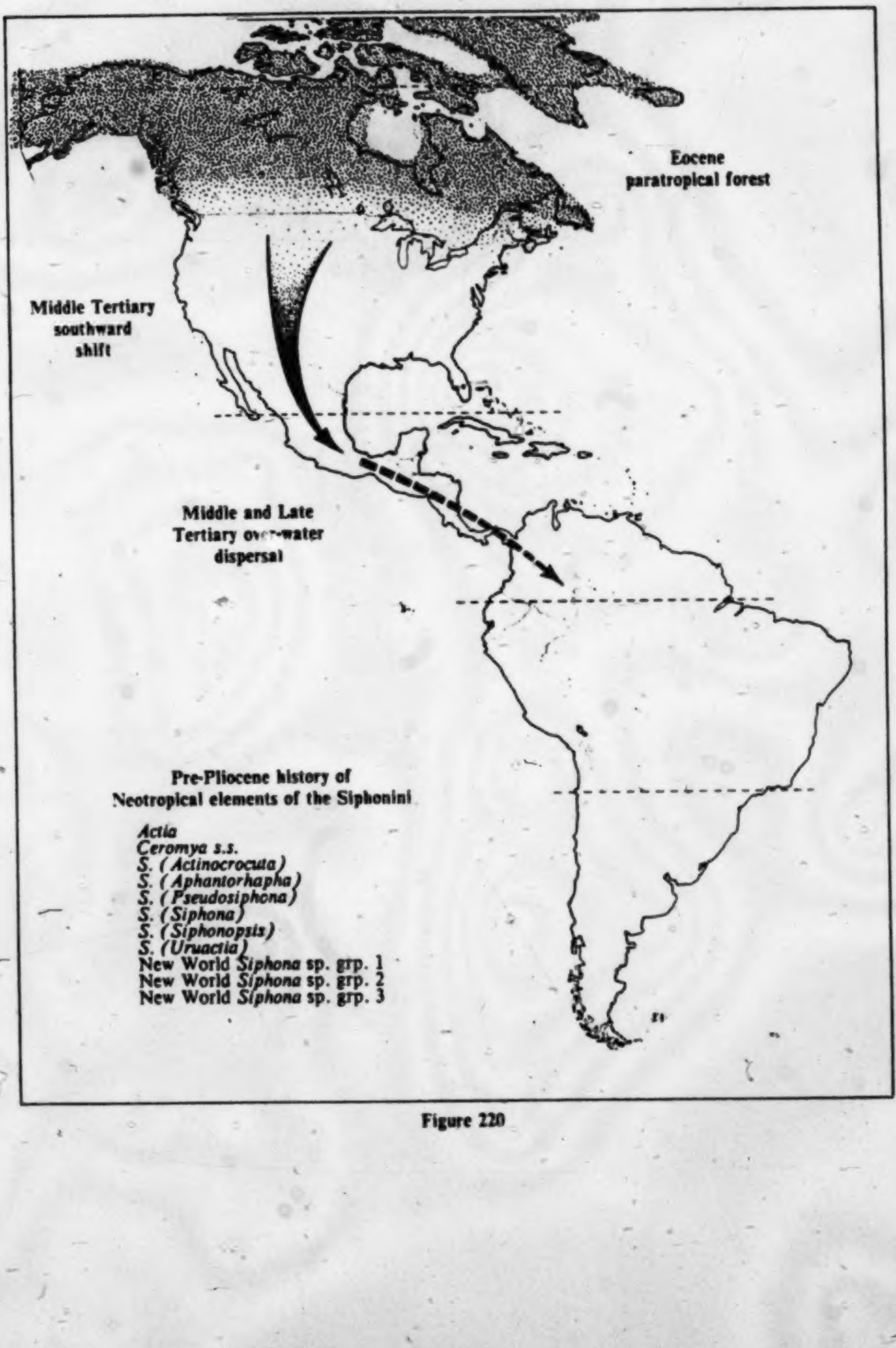

Eocene paratropical forest
Middle Tertiary southward shift
Middle and Late Tertiary over-water dispersal
Pre-Pliocene history of Neotropical elements of the Siphonini
Actia
Ceromya s.s.
S. (Actinocrocuta)
S. (Aphantorhapha)
S. (Pseudosiphona)
S. (Siphona)
S. (Siphonopsis)
S. (Uruactia)
New World *Siphona* sp. grp. 1
New World *Siphona* sp. grp. 2
New World *Siphona* sp. grp. 3

Figure 220

7. CONCLUDING REMARKS

I have set forth in this paper a revised classification of the supraspecific taxa of the Siphonini. For the first time, the markedly different classifications of the Old and New World Siphonini have been meshed. Relatively few taxonomic changes are proposed as a result of this action, except for a number of changes in rank to update and balance the classification (particularly with respect to genus group names among New World *Siphona* group taxa) and several new higher level combinations required on phylogenetic grounds.

Considerable effort was made to classify - and provide a key for identification of - Neotropical siphonines, even though most of the known species are undescribed. However, this effort is but a preliminary attempt, and apt to be inadequate for some taxa. Present categories will need to be modified, and new subgenera of *Siphona s.l.* will almost certainly need to be erected, when the diverse siphonine fauna of the Neotropical region is more completely studied and the species described.

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